Spatial and temporal determinants of samango monkey (Cercopithecus mitis erythrarchus) resource acquisition and predation avoidance behaviour

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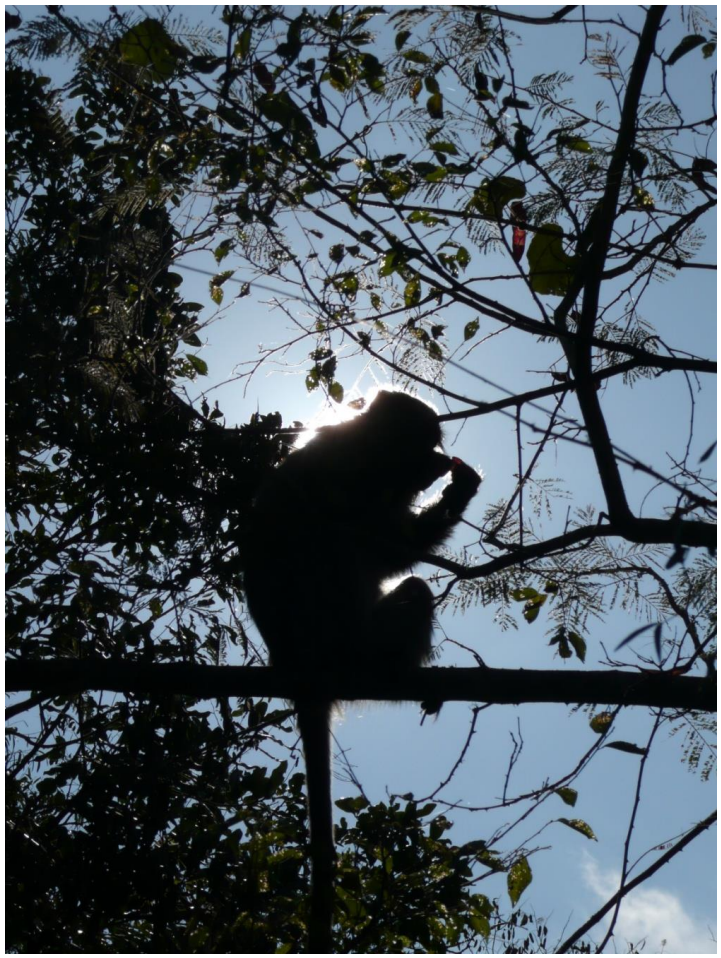

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Abstract

Food acquisition and predator avoidance are principal components of the survival strategies of all primates. However, for primates, maximising food acquisition whilst minimising predation risk is often impossible. This leads to the existence of the foraging/risk trade-off, a mechanism fundamental in shaping life histories, species interactions and ultimately community assemblage. The principal aim of this study was to investigate how samango monkeys (*Cercopithecus mitis erythrarchus*) strategically balance the foraging/risk trade-off when exposed to spatially and temporally varying resources and risk.

Data were collected on a habituated group of samango monkeys over a 12 months observational period at the Lajuma Environmental Research Centre, South Africa. The focal group are part of a population near the southerly limit of the most southerly ranging African, primarily arboreal, monkey species. A biogeographical approach was also used, utilising ecological data from 12 different populations of *C. mitis* from a number of field sites across the species' distribution.

Cold, dry winter periods were associated with increased time spent feeding and decreased in time spent resting. During winter months the samangos supplement their diet with foliar material, most likely due to the increased energetic requirements of maintaining body temperature. On a geographical scale, southern populations of samango have significantly more fruit in their diet than their more equatorial relations; whilst the opposite pattern is apparent involving the amount of animal matter consumed. On a spatial scale resources appear to be less important in determining samango ranging behaviour than the risk of predation. The study group actively avoid areas of perceived eagle predation risk, even though resources, such as food, are available in those areas. Similarly, the samangos increase time spent vigilant when in areas of high perceived eagle predation risk, but environmental factors such as visibility or food availability have little effect on vigilance.

The findings of this study indicate that a population at the edge of their species' ecological tolerance are forced to considerably adapt behaviourally to seasonally and spatially varying resources and risk. In particular, great effort is put into avoiding predation risk; by avoiding high risk areas and maintaining an adequate level of vigilance. All of this must be achieved whilst combating rival groups and maintaining a territory, ensuring adequate food can be foraged and ensuring the successful raising of the next generation.

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Chapter 1

Introduction

1.1 The foraging/risk trade-off

Food acquisition and predator avoidance are principal components of the survival strategies of most animals (Lima 1998). However, for many animals maximising food acquisition whilst minimising predation risk is impossible. For example, most animals are unable to forage and remain vigilant for predators at the same time (Underwood 1982, Lima 1998). Likewise, preferred food sources might be in areas or habitats considered higher predation risk and animals may choose to feed on lower quality foods in lower risk areas (Cowlishaw 1997). Taking greater risks may reward an individual with more food, but significantly increase the chances of being preyed upon (McPeek 2004).

The foraging/risk trade-off is fundamental in shaping life histories, species interactions and ultimately community assemblage (Wellborn et al. 1996). The different rewards and dangers in different habitats may force individuals to tackle the foraging/risk trade-off in different ways, which in turn may have important effects on natural selection. Inter-specific differences in the solution to this trade-off are thought to be an important mechanism underlying how species share similar niches, surviving on the same food sources and exposed to similar predators (Levin 1970, McPeek 1996). An excellent example is from Ecuador where both the chestnut short-tailed bat (*Carollia castanea*) and Seba's short-tailed bat (*C. perspicillata*) feed on *Piper hispidum* peppers, which ripen during the night (Bonaccorso et al. 2007). Seba's bats are better at handling the fruit, approximately 50% larger than chestnut bats and

able to out-compete chestnut bats if they forage at similar times. Chestnut bats therefore emerge much earlier in the night, before Seba's bats emerge. The disadvantage to this early emergence is an increased chance of predation by bat falcons (*Falco rufigalaris*); however, due to their small size chestnut bats are better able to avoid predation at these times. By approaching the foraging/risk trade-off in different ways, these two similar species of bat coexist in the same space, feeding on the same food and subject to the same predator.

Individuals, living solitarily, must be able to adequately monitor their surroundings whilst also maintaining foraging efficiency. This can only be achieved by efficient balancing of the foraging/risk trade-off. However, samango monkeys (*Cercopithecus mitis erythrarchus*), like most primate species, are group living, in groups of up to 65 individuals (Butynski 1990, Beeson et al. 1996, Smith et al. 2008, Houle et al. 2010, Lawes et al. 2011). Group living can significantly affect the way individuals use the foraging/risk trade-off, because by residing in groups individuals may reduce the overall level of predation risk they experience (van Schaik 1983) whilst also increasing competition for resources (Wrangham 1983). The aim of this study is to investigate how samango monkeys approach the foraging/risk trade-off in terms of the spatially and temporally varying resources and predation risk they encounter. A particular focus will be on how they utilise anti-predation strategies, such as the strategic use of habitats, vocalisations and vigilance behaviour.

1.2 Group living

There are several advantages to living in groups; these include social advantages, such as increased mate choice (Petersson & Sivinski 2003) and an improved ability to defend resources from conspecifics (Wrangham 1980, 1983). However, several studies have pointed towards anti-predation benefits as the main reason for the evolution of group living (Alexander 1974, van Schaik 1983). Living in a group

decreases an individual's probability of being predated due to the "dilution effect", where increased numbers reduce any one individual's risk of being preyed upon (Hamilton 1971, Dehn 1990), or by predator deterrence (Maisels et al. 1993). Perhaps more important is the "detection effect", where a larger group allows for more potentially vigilant individuals, increasing the chance of spotting a predator (Cresswell 1994). Individuals are able to reduce their own time spent vigilant through reliance on other members (Pulliam 1973), which may allow individuals to access resources in areas or at times otherwise considered to incur too high a risk of predation.

The majority of primates live in social groups, ranging in size from two (e.g., *Loris* spp.) to over 300 (e.g. *Theropithecus gelada*) (Clutton-Brock & Harvey 1977). Group sizes show large variation within species, with groups varying from 15 to 150 individuals in species such as olive baboons (*Papio anubis*) (Dunbar 1992). Group composition also varies between species, for example many species live in groups which contain multiple adult males and females; whereas, others may live in single-male, multi-female groups (Kappeler & van Schaik 2002). These different group compositions have also been recorded within the same species, for example in red howler monkeys (*Alouatta macconnelli*) (Pope 1998) and mountain gorillas (*Gorilla beringei*) (Robbins 1995). The causes of such variation within these species are often attributed to changing environmental conditions. All of these differences in group composition have the potential to significantly affect the way in which individuals within groups approach the foraging/risk trade-off.

Using an ecological modelling approach on a variety of primate species, Wrangham (1980) suggested that group living confers a stronger advantage for resource defence than as an anti-predator strategy. Several studies have since come to the opposite conclusion, finding that predator defence is the most important basis for the existence of group living in primates. For example, a number of studies have concluded that group living can only confer disadvantages in terms of competition for resources, and that an anti-predator hypothesis is the only possible cause of primate group living

(van Schaik 1983, Terborgh & Janson 1986, Dunbar 1988). Isbell (1991) showed that large groups confer a strong disadvantages in terms of intra-group resource competition, a conclusion confirmed by Dunbar (1992) in a study investigating resource competition in baboon groups. Taken together, these studies suggest that predation generally sets the threshold for minimum group size (van Schaik 1983, Dunbar 1988), whilst intra-group competition sets the upper limit (van Schaik 1983, Dunbar 1992).

1.3 Resource availability

1.3.1 Local spatial variation

Variation in abiotic factors such as aspect, altitude and slope can have important effects on the plant assemblage in an area, often leading to a variety of distinct habitat types containing very different plant species (Ricklefs 1987, Musina & Rutherford 2006). Such variation has important consequences for food availability. Low food availability can result in reduced rates of fecundity, growth and survival for animals, and such effects have been observed in a number of primate species including yellow baboons (*Papio cyanocephalus*) (Altmann et al. 1977), chacma baboons (*P. ursinus*) (Hamilton 1985), Japanese macaques (*Macaca fuscata*) (Hanya et al. 2004) and saddle-backed tamarins (*Saguinus fuscicollis*) (Goldizen et al. 1988). Therefore, all primate groups maintain home ranges which encompass a large enough area to allow them to find adequate food to survive and reproduce (Mitani & Rodman 1979). Many primate species have been observed varying their utilisation distribution or ranging behaviour dependent upon local food availability (for example Waser 1977, Stanford 1991, Zhang 1995, Doran 1997, Hanya 2004, Volampeno et al. 2011).

While food availability is an important consideration for primates, other spatially variable resources may also affect primate behaviour. A number of studies have

reported primates to vary their ranging to access spatially variable resources such as water sources (De Gama-Blanchet & Fedigan 2006, Ferrari & Hilario 2012) and refuges from predators (Cowlishaw 1997). Arboreal species may avoid areas of low tree cover or lower canopy height for reasons such as a lack of food availability or a higher predation risk associated with more open areas (Salter et al. 1985, Bitty & McGraw 2007). Primates must consider the foraging/risk trade-off when choosing where to forage and may choose to avoid areas considered too high risk of predation even though resources may be available to them there (Willems & Hill 2009b).

The examples above mention how spatially varying resources may affect primate behaviour but they do not take into account the potential for temporally varying resource availability. All areas populated by primates are subject to a seasonal climate, often experiencing significant seasonal variations in factors such as temperature and rainfall (Hijmans et al. 2005). Therefore, when considering the effect of resource availability on primate behaviour it is important not only to consider how the resources vary spatially but also on a temporal scale.

1.3.2 Local seasonal variation

Seasonal variation in temperature and light intensity becomes more pronounced at higher latitudes (Berger & Loutre 1991, Hijmans et al. 2005) and many areas also experience highly seasonal rainfall patterns (Hijmans et al. 2005). Such climate variation can have marked effects on the fruiting behaviour of plants (Conklin-Brittain et al. 1998, Wrangham et al. 1998). Seasonal food availability can have important effects on primate foraging behaviour in terms of ranging (Waser 1977, Hanya 2004), activity budgets (Garber 1993, Doran 1997, Chaves et al. 2011) and diet composition (Milton 1980, Garber 1993, Peres 2000). This, in turn, can have important effects on how primates approach the foraging/risk trade-off. For example, during the dry season, when naturally available fruit was low, common squirrel monkeys (*Saimiri sciureus*) increased the amount of time spent feeding on artificial platforms located in higher predation risk areas (Stone 2007). These results suggest

that the squirrel monkeys were willing to accept a higher risk of predation to find enough food at times of low food availability.

These studies suggest that seasonal climatic variation can have important effects on a variety of primate behaviours, particularly foraging behaviour. One way to measure how strong this effect is would be to compare populations of the same species resident in areas with differing climates. Even though they may be genetically similar, members of the same species, experiencing different environmental conditions, may be forced to adapt behaviourally to such conditions in very different ways.

1.3.3 Geographical variation

Several primate species span very large distributions, covering a large number of habitat types (Wolfheim 1982). For example, yellow baboons and vervet monkeys (*Chlorocebus aethiops*) have distributions which cover many thousands of square kilometres (Kingdon et al. 2008a, Kingdon et al. 2008b). In a study of 15 baboon populations ranging from Ethiopia to South Africa, Hill & Dunbar (2002) showed that in areas where fruit might be limiting, baboons use leaves and subterranean foods to supplement their diet. Similarly, mountain gorillas have been shown to consume more leaf material and spend more time resting in areas of lower overall fruit availability (Lehmann et al. 2008). These studies highlight the important effect varying climatic conditions can have on primate behavioural ecology. Understanding the ways in which members of similar species adapt behaviourally to different environmental conditions is vital in understanding species' distributions and evolution (Mittelbach et al. 2007).

To understand the ecology, distribution and evolution of a species it is important to attempt to understand what factors drive behaviour. This may be on a local scale in terms of spatially varying resources, or on a geographical scale in terms of strongly differing climates between populations. Without understanding how a species

responds to resource availability, it is extremely difficult to understand the potential effects of other factors such as predation risk.

1.4 Predation risk

1.4.1 Space

Landscapes vary in factors such as water availability, slope and altitude which in turn leads to variation in plant assemblage and habitat structure (Ricklefs 1987, Musina & Rutherford 2006). Furthermore, the risk of predation varies with environmental factors such as the degree of cover provided by vegetation, or the accessibility of an area to predators (e.g. cliff face vs. open grassland) (Mcnamara & Houston 1987, Lima 1998, Brown & Kotler 2004). With variation in both food availability and predation risk animals will often be forced to vary how they approach the foraging/risk trade-off spatially.

Examples of the food availability/risk trade-off have been observed in a variety of species. Orb web spiders (*Argiope keyserlingi*) have been observed to prefer areas of lower foraging potential because of their associated reduced risk of bird predation (Blamires et al. 2007). Similarly, larval tiger salamanders (*Ambystoma tigrinum*) have been observed to avoid littoral areas at times when predation risk from diving beetles (*Dytiscus dauricus*) is high, although their preferred food source is present in those areas (Holomuzki 1986). In experiments on captive heteromyid rodents, Longland & Price (1991) observed the avoidance of open habitats, which were associated with higher risk from great horned owls (*Bubo virginianus*). Again, a similar pattern has been observed in bottlenose dolphins (*Tursiops aduncus*) which have been shown to avoid their preferred feeding areas during warm months when tiger shark (*Galeocerdo cuvier*) predation risk in those areas is higher (Heithaus & Dill 2002).

In one of the first studies to investigate the habitat use trade-off in primates, Cowlishaw (1997) observed that chacma baboons in Namibia, living under risk of predation from leopards (*Panthera pardus*) and lions (*P. leo*), choose to forage in areas of low risk but low food quality, rather than in higher food quality, higher risk areas. The effect of predation risk did not just affect foraging behaviour, with the monkeys also choosing to rest and groom in lower risk areas. Similarly, Hill & Weingrill (2006) observed that chacma baboons in South Africa avoided areas considered high risk of leopard predation, and when foraging in high risk areas would try to feed in locations with high visibility or with nearby potential refuges. More recently in a study on vervet monkeys, Willems & Hill (2009b) observed that the monkeys actively avoided areas of high perceived leopard and baboon predation risk, although there were potentially important resources available in those areas.

Variation in predation risk over a landscape can have significant effects on the community assemblage and diversity in those areas. For example, in the Qingliangfeng Mountains, China, Reeves' muntjacs (*Muntiacus reevesi*) prefer areas of high shrub density where they can remain concealed from predators. In contrast, wild boars (*Sus scrofa*) utilise the more open areas because they can employ running as an escape strategy (Lu et al. 2007). In Ladakh, India, blue sheep (*Pseudois nayaur*) use areas of cliff where their short legs give them an advantage against predators, whereas Tibetan argali (*Ovis ammon hodgsoni*) use the more open areas because their longer legs allow them to move faster over more open ground (Namgail et al. 2004). An understanding of the spatial distribution of resources and risk is essential to understand a group's ranging or behavioural ecology fully. However, for an individual it is not simply the case of associating each area with a certain level of risk, since there is also the potential for risk to vary considerably on a temporal scale.

1.4.2 Time

Risk can vary over time for several reasons. In a review of resource partitioning, Schoener (1974) came to the conclusion that predators are highly likely to prefer

certain times of day for hunting. This may be because prey species show peaks of activity at certain times of the day or because certain conditions aid the predator's ability to hunt. Many predators have evolved specialised morphological characteristics which benefit their preferences, such as echolocation in bats, which aids nocturnal hunting (Jones & Teeling 2006). Similarly, as ambush predators, leopards tend to prefer nocturnal hunting because of the added advantage in concealment (Bailey 1993). In contrast, the risk of predation by African black eagles on rock hyrax (*Procavia capensis*) in the Augrabies Falls National Park, South Africa, is highest around midday, when thermals create optimal conditions for eagles to hunt (Druce et al. 2006). Shultz & Noë (2002) studied seven different Cercopithecine and Colobine species in Tai National Park, Cote d'Ivoire. They observed that eagle activity was highest in the mornings and evenings and this correlated with a higher rate of monkey alarm calls.

Predation may be an important factor contributing to daily prey activity patterns. For chacma baboons, increased predation risk prohibits their usage of the nocturnal phase, and therefore they are an obligate diurnal species (Hill 2004). Similarly, the cathemeral lifestyles of many lemurs (*Lemuroidea* spp.) may be a specific adaptation to predation risk from fossa (*Cryptoprocta ferox*) (Colquhoun 1998). Such species are responding behaviourally to the active periods of their predators by choosing to forage at times when risk is lower.

Predation risk may also vary seasonally (Rasmussen 2005). This can occur for several reasons, such as predators requiring more food due to the birth of offspring (Bujoczek & Ciach 2009), a reduction in other prey animals due to migration (Lee & McCracken 2005) or the increase of vegetative cover for predators in the wet season (Smuts 1978). Furthermore, times of low food availability may force animals to take higher risks to obtain food. For example, during the dry season, when vegetative cover was at its lowest, mongoose lemurs (*Eulemur mongoz*) and brown lemurs (*E. fulvus*) shift from diurnal to more crepuscular activity cycles to counteract the increased risk from raptors during the day (Rasmussen 2005).

Primates must survive in landscapes are often highly variable in food availability and predation risk on both spatial and temporal scales. Decisions have to be made affecting the foraging/risk trade-off, which have potentially important effects on survival and reproduction. However, even if an individual is able to balance this trade-off in the most efficient manner possible, there will always be times where it must forage in areas or times where there is a higher risk of predation. In an attempt to minimise predation in these situations primates have evolved a variety of different anti-predator behaviours, such as crypsis (Janson 1998a) or aggressively challenging a predator (Gursky 2005). However, one of the most ubiquitous and important anti-predator behaviour is vigilance, allowing an individual time to escape or adopt a defensive position should a predator be spotted (Bednekoff & Lima 1998).

1.4.3 Vocalisations

Many primate species use predator-specific alarm vocalisations, to warn other members of their group of an imminent threat (Fedurek & Slocombe 2011). The first study to investigate primate alarm calls was Struhsaker (1967a), investigating acoustically distinct vocalisations of vervet monkeys; subsequently, using play-back experiments Seyfarth et al. (1980) concluded that these calls were also predator-specific, signifying arboreal or terrestrial threats. Since these seminal studies, functionally referential alarm calls have been described in a large variety of primate species including chimpanzees (*Pan troglodytes*) (Crockford & Boesch 2003), Diana monkeys (*Cercopithecus diana*) (Zuberbuhler et al. 1997), putty-nosed monkeys (*Cercopithecus nictitans*) (Arnold & Zuberbuhler 2006), guereza colobus monkeys (*Colobus guereza*) (Schel et al. 2010), black-fronted titi monkeys (*Callicebus nigrifrons*) (Casar et al. 2012), and ring-tailed lemurs (*Lemur catta*) (Macedonia 1990). These calls often denote the direction of a threat, for example arboreal or terrestrial, or may denote a specific type of predator, for example a raptor, regardless of the position of the predator. The main advantage of these functionally referential calls appears to be the potential for specific escape responses. For example, a response to an alarm call denoting an arboreal threat might be to drop into

understory foliage which provides better cover from such a predator (Cords 1987). Thus alarm vocalisations are an important anti-predation tool used by a range of different primate species. However, the usefulness of alarm vocalisations as an anti-predator strategy depends upon individuals remaining vigilant, to allow sufficient time to warn others of potential threats.

1.5 Vigilance

1.5.1 Vigilance strategies

Most animals are unable to forage and remain vigilant at the same time (Underwood 1982, Lima 1998). Therefore, individuals are often forced to trade-off between time foraging and time spent vigilant. Individuals can apply various strategies when foraging under higher predation risk to counteract this problem, all of which have their own advantages and disadvantages. One option would be to allocate more time to remaining vigilant whilst foraging. This will increase overall time spent foraging and therefore reduce time available for other activities such as resting or socialising. This pattern has been observed in alpine ibex (*Capra ibex*) where lactating mothers have been shown to spend less time resting to allow them to increase time spent vigilant whilst foraging (Toigo 1999). Secondly, individuals may increase vigilance but reduce time available to foraging, with potential consequences such as starvation. A good example of this strategy is employed by female elk (*Cervus canadensis*) and bison (*Bison bison*). In 1994 wolves (*Canis lupus*) were reintroduced to Yellowstone national park. Female elk and bison in the vicinity of this reintroduction were observed to spend significantly more time vigilant and less time foraging than populations in non-wolf areas of the park (Laundre et al. 2001, Childress & Lung 2003). Finally, an individual could keep vigilance at the same level, or even reduce it, minimising the time spent foraging in high risk areas. Individuals are then able to allocate more time to activities where they can maintain a high level of vigilance,

move to a refuge or move to a different area considered lower risk of predation. This strategy was referred to as "risk-reckless" by Fraser & Huntingford (1986) in their study on three-spined sticklebacks (*Gasterosteus aculeatus*).

As predation risk is likely to vary over space and time, primates should vary their vigilance strategy accordingly. Vigilance plays an important role in the anti-predator behaviour strategies of many different primate species and studies investigating the subject have included, amongst others, apes (Watts 1998, Kutsukake 2006, 2007), baboons (Hall 1960, Alberts 1994, Cowlishaw 1998), macaques (Maestripieri 1993, Chalmeau et al. 1998), guenons (Cords 1990, 1995, Bshary & Noë 1997), capuchins (de Ruiter 1986, Rose & Fedigan 1995, Burger 2001, Hirsch 2002), tamarins (Smith et al. 2004, Stojan-Dolar & Heymann 2010a, b) and lemurs (Gould 1996, Gould et al. 1997). For example, when studying two groups of brown capuchin monkeys (*Cebus apella*) known to be under different predation pressures, Hirsch (2002) observed a significantly lower proportion of time spent vigilant in the group under lower predation pressure. Similarly, chacma baboons decrease vigilance at times they consider less risky, such as when they are closer to refuges (Cowlishaw 1998).

There is strong evidence for a foraging/vigilance trade-off in primates, with a frequent result observed being that the proportion of time spent vigilant whilst feeding is lower than during other activities such as resting (Cords 1995, Chalmeau et al. 1998, Cowlishaw 1998, Treves et al. 2001, Kutsukake 2006, Stojan-Dolar & Heymann 2010a). However, the foraging/vigilance trade-off is not as simple as the difference between vigilance potential during different activities. Teichroeb & Sicotte (2012) observed an increase in ursine colobus monkey (*Colobus vellerosus*) vigilance whilst feeding when lower in the canopy, indicating a higher perceived risk at those heights. Stojan-Dolar & Heymann (2010a) observed that moustached tamarins (*Saguinus mystax*) decrease their vigilance whilst feeding when there were more conspecifics nearby, indicating that more nearby individuals decrease the risk of predation. This pattern has also been observed in other species, such as chacma baboons (Cowlishaw 1998), white-faced capuchins (*Cebus capucinus*) (Rose &

Fedigan 1995, Burger 2001) and brown capuchins (Hirsch 2002), black howler monkeys (*Alouatta pigra*) (Treves et al. 2001), and Thomas' langurs (*Presbytis thomasi*) (Steenbeek et al. 1999). This effect may be due to increased resource competition, forcing individuals to spend more time foraging, or perhaps more likely may be due to decreased predation risk caused by more potentially vigilant individuals.

Within group vigilance

Many previous primate vigilance studies have used group size as the unit upon which they investigate the effect nearby conspecifics have on an individual's vigilance behaviour (Roberts 1996). Although a few primate studies have discerned a significant effect of increasing group size on vigilance, either positive (de Ruiter 1986, Teichroeb & Sicotte 2012) or negative (Burger 2001), the majority observe no significant correlations (Rose & Fedigan 1995, Treves 1998, Jack 2001, Treves et al. 2001, Stojan-Dolar & Heymann 2010a). It has been suggested that the reason for this lack of effect is conflicting vigilance demands of predation risk and risk from conspecifics (Janson 1998b), which may originate from a variety of reasons including the risk of infanticide (Hrdy 1979) or the establishment of dominance hierarchies (Bernstein 1976). However, it has been suggested that varying group size does not provide a good basis for investigating the effect of the conspecific effect on vigilance behaviour and group density might be a better option (Elgar 1989, Treves 1998). This would explain why some studies observe significant effects of group density, but no effect of group size, on vigilance behaviour (Rose & Fedigan 1995, Treves 1998, Treves et al. 2001, Stojan-Dolar & Heymann 2010a).

Several primate studies have investigated the effect of group density on vigilance behaviour with the majority showing that increasing group density correlates with a reduction in individual vigilance (e.g. van Schaik & van Noordwijk 1989, Rose & Fedigan 1995, Cowlishaw 1998, Treves 1998, Steenbeek et al. 1999, Treves et al. 2001, Stojan-Dolar & Heymann 2010a, Teichroeb & Sicotte 2012). The opposite effect

though, of higher group density causing an increase in individual vigilance, has been observed in brown capuchin monkeys (Hirsch 2002), red colobus monkey males (*Procolobus badius*) (Treves 1998) and chimpanzees (Kutsukake 2007). Thus, although there is the potential for nearby neighbours to cause an individual to be more vigilant, this appears to not be the case in the majority of primate species. This suggests that benefits of improved detection potential, caused by nearby conspecifics, outweigh the risks posed by those conspecifics. In fact, many primate species show very little intra-group aggression (Isbell 1991, Cords 2002a), indicating decreased vigilance due to the presence of nearby individuals to be likely response to lower predation risk.

To survive and reproduce animals must vary their approach to both their foraging behaviour and anti-predation behaviour in response to spatially and temporally varying resources and risk. An individual is rarely able to maximise foraging potential whilst minimising predation risk, which leads to the foraging/risk trade-off. Not being able to balance this trade-off efficiently may lead to a reduction in foraging potential or an increase in mortality risk, which can have extremely costly effects on an individual's fitness. The use of these trade-offs are apparent in a range of different species both primate and non-primates and have significant effects in shaping the ecological landscape and evolution.

1.6 Samango monkeys

Samango monkeys are one of the largest distributed African non-human primate species (Wolfheim 1982). They are present in many forest habitats ranging from Ethiopia in the north to South Africa in the south. Given this large distribution it is surprising that as a species they remain relatively understudied. Much is known regarding the behavioural ecology of other large ranging species, such as chacma baboons (Dunbar 1992, Hill 1999, Johnson 2003) or vervet monkeys (Struhsaker

1967b, Seyfarth et al. 1980, Willems 2007), but comparatively less is known regarding the behavioural ecology of samangos. This thesis represents a long term observational study of a group of South African samango monkeys, and looks to address a number of the current gaps in the literature.

The large geographical distribution of samangos allows an almost unique opportunity to observe how an arboreal monkey species is able to adapt behaviourally to survive in differing locations and under different environmental conditions. However, no attempt has previously been made to investigate the determinants of variation in samango monkey behavioural ecology over such a geographical scale. To attempt to fully understand a species' ecology, especially a large ranging species, it is important to encompass populations from different locations within that range, otherwise a very narrow ecological view is used to represent an entire species. For example, many studies investigating samango monkey behavioural ecology have originated from populations within Kenya and Uganda (e.g. Rudran 1978, Cords 1987, Butynski 1990, Cords & Chowdhury 2010). Such populations are centrally located within the distribution of the species (Kingdon et al. 2008c). Whilst this allows for a detailed view of certain subspecies, this leaves the overall view of the species potentially lacking; and whilst it is important to understand the ecology within such populations, comparatively little is known about populations located closer to the edge of the species' distribution. By studying such edge populations it is possible to investigate the degree to which individuals are forced to adapt behaviourally to survive at the edge of their species' ecological tolerance (Sexton et al. 2009).

Predation risk has been suggested as an extremely important determinant of primate behavioural ecology, and therefore evolution (van Schaik 1983, Anderson 1986, Dunbar 1988, Zuberbuhler 2007); however, within samango monkeys the potential effect of predation is still not well understood. Samango monkeys, throughout their range, are exposed to risk from a variety of arboreal and terrestrial predators (Skorupa 1989, Struhsaker & Leakey 1990, Wrangham et al. 1990, Mitani & Watts 1999, Hayward et al. 2006, Foerster 2008). Whilst some studies have investigated the

determinants of samango vigilance behaviour (Cords 1990, 1995, Treves 1999, Cowlishaw et al. 2004, Gaynor & Cords 2012) and alarm vocalisations (Brown 1989, Papworth et al. 2008); there is still the need to understand, in more detail, how predation risk can affect samango behavioural ecology. Understanding the importance predators have in determining how samangos behave is vitally important in extending our knowledge of the evolution of the species and Cercopithecines in general (Anderson 1986).

1.7 Aims

Samango monkeys have a large distribution throughout much of Central and Southern Africa (Kingdon et al. 2008c). The study group is located near the southern limit of this range and so represent a population at the edge of the ecologically tolerable conditions for samango monkeys. The primary aim of this thesis is to investigate how this group of samango monkeys respond behaviourally to the varying environmental conditions and predation risk they encounter and this will be achieved through the instigation of a number of different objectives.

The first objective is to investigate how the samangos vary their basic ecology, such as activity budgets and diet composition over different seasons. This includes a relatively cold, dry winter, which more equatorially located populations do not experience. It is expected that in the dry, cold winter the samango monkeys will increase time spent feeding on leaves, and will decrease time spent feeding on fruit. This will most likely be due to a decrease in fruit availability during winter months. Another aim of the thesis is to further investigate the ability for samangos to survive difficult climates. This will be achieved by taking a biogeographical approach and comparing the diet compositions of different study populations throughout the species' range. It is expected that samangos resident in more equatorial populations

will have a higher proportion of fruit in their diet, compared to more southerly populations found in countries such as South Africa.

Another important element of this thesis is investigating how the samangos vary their behaviour dependent upon variation in risk, especially predation risk. Resident at the study site, in high densities, are two known samango monkey predators, leopards and eagles (Willems 2007). An important objective of this thesis is to investigate how the risk of predation, from such predators, may cause the samangos to vary their anti-predation behaviour, both in terms of their strategic use of space and their vigilance behaviour. For example, it is expected that the samangos will avoid using areas they consider high risk of leopard and eagle predation, even though those areas may contain beneficial resources. Vigilance behaviour will be investigated in detail, as it is an important anti-predation behaviour for most, if not all, primates (Baldellou & Henzi 1992, Cords 1995, Cowlishaw 1998, Treves 2000). It is expected that the monkeys will decrease proportion of time vigilant whilst foraging, compared to when resting. There also is a pattern of decreasing time vigilant, with increasing numbers of nearby conspecifics. Vigilance will also be investigated in terms of how levels of vigilance vary spatially. In this regard, it is expected that the samango monkeys will increase time spent vigilant when in areas they consider high risk of predation. This is also likely to be directional; for example, it is expected they will increase time spent looking upwards in areas of high perceived eagle predation risk.

1.8 Thesis outline

The methodology chapter (Chapter 2) is a description of the study site and species and contains an overview of some of the ecological and behavioural sampling methods used in the study. Chapter 3 presents the basic behavioural ecology of the study group and how it varies seasonally. Chapter 4 is an investigation into how characteristics of behavioural ecology, specifically diet composition, vary throughout

the distribution of the species and how climate affects this variation. Chapter 5 is an investigation of the spatial variation in perceived risk both from predators and conspecific groups and how these risks and the distribution of resources affect ranging behaviour. Chapter 6 looks at possible intra-group effects on vigilance behaviour, such as height in trees and the close proximity of conspecifics. Chapter 7 investigates spatial variation in different types of vigilance behaviour, for example looking upwards, and how this relates to perceived risk and other factors. Finally in Chapter 8 the results of all the previous chapters will be integrated, for a general discussion on their importance regarding samango behavioural ecology and evolution.

Chapter 2

Methodology

2.1 Study species

Cercopithecus mitis (Wolf, 1822) commonly known as samango, Sykes' or blue monkeys (throughout this thesis they shall be referred to as samango monkeys or samangos) are medium sized, arboreal guenons with a mean adult female weight of approximately 4.4kg and adult male weight of approximately 7.6kg (Harvey et al. 1987). They have an average life-span of around 27 years in the wild (based on adult female data (Cords & Chowdhury 2010)). Females reach sexual maturity at around 62 months (Harvey et al. 1987), with a gestation period of 140 days (Rowell 1970) and males at approximately 72 months (Harvey et al. 1987). Weaning occurs after 30 months (Cords 1988) and the female inter-birth interval is 24-54 months (Cords 1987).

Samangos form single-male, multi-female groups (Rudran 1978, Henzi & Lawes 1987), a pattern typical of forest guenons (Struhsaker 1969), with group sizes ranging from 4-65 (Butynski 1990, Beeson et al. 1996, Smith et al. 2008, Houle et al. 2010, Lawes et al. 2011). However, it is not uncommon for groups to have more than one resident male and during breeding season the number of males in a group can increase (Henzi & Lawes 1987, Cords 2002b). In the Kakamega Forest, Kenya, this occurs in 23% of breeding seasons (Cords 2002b), and it is not uncommon for four or five extra-troop males to enter the group during this period. Resident male tenure can vary from 14-94 months (Cords 1988, Macleod 2000). Aggressive interactions between individuals in a group are generally rare; the average female has an agonistic

interaction only every 2.2 hours (Cords 2002a). This seemingly peaceful nature contributes to the species name *mitis*, Latin for gentle.

2.1.1 Vocalisations

Samangos display a variety of acoustically distinct vocalisations. Juveniles and adult females regularly "grunt", used as intra-group contact calls (Rudran 1978) and will occasionally use "hacks" and high pitched "chirps" as alarm signals (pers. obs.). Adult males use different vocalisations. The most regular vocalisation is the "boom" call. This call is deeply resonant with a frequency as low as 108Hz (Marler 1973). Although it can be heard up to 1km away (Brown 1989) the characteristics of the "boom" call suggest its likely use is maintaining group cohesion (Waser & Waser 1977). Less regularly heard is the adult male's loudest call, the "pyow", a loud, resounding call which can be heard over 1.5km away. The most likely function of the "pyow" call is to maintain spacing between different troops (Aldrich-Blake 1970); however, one study has observed the "pyow" being used as a leopard-specific alarm call (Papworth et al. 2008). The final adult male vocalisation is the step onset, low frequency "ka" call (Marler 1973), which is referred to as a "ka-train" when strung together. This call has been well studied and is now understood as an alarm call referring to an aerial threat, such as raptors (Brown 1989, Papworth et al. 2008).

2.1.2 Distribution

Samango monkey distribution is throughout much of central and east Africa: ranging from Ethiopia in the north of their range, Angola to the west, and as far south as the Eastern Cape Province of South Africa (Figure 2.1). The distribution appears to be limited by the Itimbiri and Zaire-Lualaba River systems (Colyn 1987, 1988, Wilson & Reeder 1993). As an arboreal species their distribution is patchy and restricted to areas of forest. *C. mitis* is the most southerly ranging, primarily arboreal, African monkey species (Wolfheim 1982).

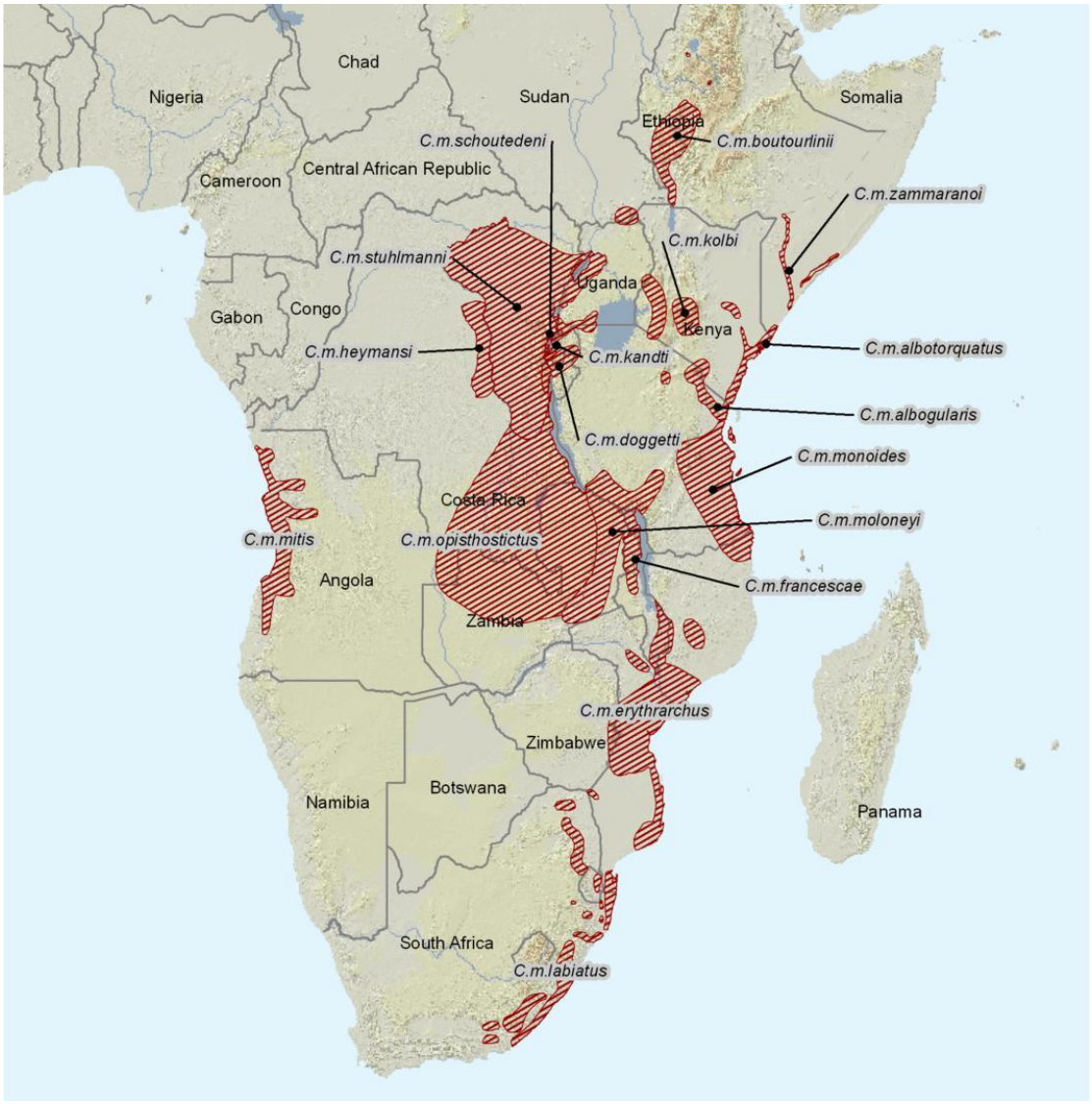

Figure 2.1 Distribution of *C. mitis* subspecies (Kingdon et al. 2008c).

2.1.3 Taxonomy

Due to such a large distribution the taxonomy of the *C. mitis* group is debated. For many the years the various populations were grouped under two main species: *C. albogularis* and *C. mitis* (Dandelot 1971, Napier 1981). This then increased to four species to include separate species of *C. doggetti* and *C. kandti* (Kingdon 1997, Groves 2001), although the number of sub-species corresponding to each taxon varied. Subsequently, after studying the literature and specimens at the Natural History

Museum in London, Grubb (2001) came to the conclusion that all the populations were so morphologically similar they should be grouped under 16 sub-species, in one species (*C. mitis*) (see also Grubb et al. 2003). Currently, the IUCN recognise these 16 sub-species plus *C. m. zammaronoi* (Kingdon et al. 2008c) after a study in Somalia gave sufficient evidence for the inclusion as a separate sub-species (Gippoliti 2006). See Table 2.1 for the breakdown of historical sub-species decisions.

Table 2.1 Number of sub-species ascribed to each of four *Cercopithecus* species in various publications.

Study	Dandelot 1974	Napier 1981	Kingdon 1997	Groves 2001	Grubb 2001	Kingdon 2008
Albogularis	11	2	1	12	0	0
Mitis	8	20	21	2	16	17
Doggetti	0	0	1	1	0	0
Kandti	0	0	1	1	0	0

As a species the overall conservation status of *C. mitis* is "least concern" with a decreasing population trend (Kingdon et al. 2008c). However, when the 17 separate sub-species are considered: two are classified "critically endangered"; one "endangered"; three "vulnerable"; one "near threatened", two "data deficient" and only the remaining eight "least concern" (Table 2.2) (Kingdon et al. 2008c). 42% of known samango monkey populations exist in forests of less than 500ha (Lawes 2002), illustrating just how many samango populations are truly at risk of extinction.

Table 2.2 The 17 sub-species of *C. mitis* recognised by the IUCN (Kingdon et al. 2008c).

Species name	Common name	Conservation status
C. m. albogularis (Sykes, 1831)	Zanzibar Sykes' monkey	Least concern
C. m. albobtorquatus (de Pousargues, 1896)	Pousargues' Sykes' monkey	Vulnerable
C. m. boutourlinii (Giglioli, 1887)	Boutourlini's blue monkey	Vulnerable
C. m. doggetti (Pocock, 1907)	Doggett's blue monkey	Least concern
C. m. erythrarchus (Peters, 1852)	Stairs' white-collared monkey	Least concern
C. m. francescae (Thomas, 1902)	Red-eared Sykes' monkey	Data deficient
C. m. heymansii (Colyn & Verheyen, 1987)	Lomami river blue monkey	Near threatened
C. m. kandti (Matschie, 1905)	Golden guenon	Endangered
C. m. kolbi (Neumann, 1902)	Kolb's white-collared monkey	Least concern
C. m. labiatus (Geoffroy-Saint, 1842)	Samango monkey	Vulnerable
C. m. mitis (Wolf, 1822)	Pluto monkey	Data deficient
C. m. moloneyi (Sclater, 1893)	Moloney's white-collared monkey	Least concern
C. m. monoides (Geoffroy-Saint & Hilaire, 1841)	Tanzania Sykes' monkey	Least concern
C. m. opisthostictus (Sclater, 1894)	Rump-spotted blue monkey	Least concern
C. m. schoutedeni (Schwarz, 1928)	Schouteden's blue monkey	Critically endangered
C. m. stuhlmanni (Matschie, 1893)	Stuhlmann's blue monkey	Least concern
C. m. zammaronoi (De Beaux, 1923)	Zammarano's monkey	Critically endangered

2.2 Study site

2.2.1 Location

Field work was conducted over a 16 months period at the Lajuma Environmental Research Centre; a 4.3km^2 area study site collaboratively run by Dr Russell Hill (Durham University) and Prof Ian Gaigher (Venda University), in the western part of the Soutpansberg Mountain Range, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S; Figure 2.2). In 1997 the research centre was granted the status of Natural Heritage Site due to its high levels of biodiversity. Lajuma is part of the Soutpansberg Conservancy, the 50km^2 Thavha Ya Muno Private Nature Reserve and the UNESCO Vhembe Biosphere Reserve; a 30,701km^2 area stretching from the Botswana, Zimbabwe and Mozambique borders in the north and west, east to the Kruger National Park area north of the Shingwedzi river, and just south of the Blouberg and Soutpansberg ranges.

Figure 2.2 Map of South Africa showing Soutpansberg Mountains (red) and Lajuma (white arrow) (Willems 2007).

2.2.2 Topography and geology

The Soutpansberg Mountain Range, part of the Waterberg Supergroup, is the most northerly mountain range in South Africa, extending from the Kruger National Park to the Blouberg Mountain (23°05'S & 29°17'E to 22°25'S & 31°20'E), covering a distance of approximately 210km at a width of 60km at its widest and 15km at its narrowest (overall ~6800km^2). Altitude ranges from 200m to 1748m. At Lajuma on site elevation varies from 1150m up to high peak Mount Letjume at 1748m, which is at the apex of the Soutpansberg range. It is estimated that the Soutpansberg strata were deposited between 1974mya and 1800mya (Cheney et al. 1990) as an east-west asymmetrical rift along the Palala Shear Belt (Brandl 2003). This belt formed due to a collision between the Limpopo belt in the north and the Kaapvaal craton from the south (Bumby 2000). There are two major volcanic units in the Soutpansberg group: the Mgwanedzi Formation and the Sabasa Formation, and rock composition is equal amounts of sub-aerial sediments (arkoses, arenites, conglomerates) and volcanic sediments (Crow & Condie 1990). The substrate is characterised by an acidic sandy soil derived from sandstone, quartzite or shale (Werger & Coetzee 1978).

2.2.3 Climate

Local climate is classified as temperate/mesothermal, with cool, dry winters from April-September and warm to hot, wet summers from October-March (Willems 2007). Due to its east-west orientation and moisture-laden air from the Indian Ocean, the Soutpansberg receives orographic precipitation (Kabanda 2003). Rainfall can however be extremely variable, an important town in the area Makhado, from 1965-1971 received an mean of 571mm per year, whereas from 1979-1988 the mean was 1027mm (Mostert 2007).

Using data collected from a variety of sources for the period 1950-2000, Hijmans et al. (2005) created an interpolated high resolution (30 arc s) world climate map, detailing mean precipitation and temperature information. Using this climate map data were extracted from the location of Lajuma (Figure 2.3).

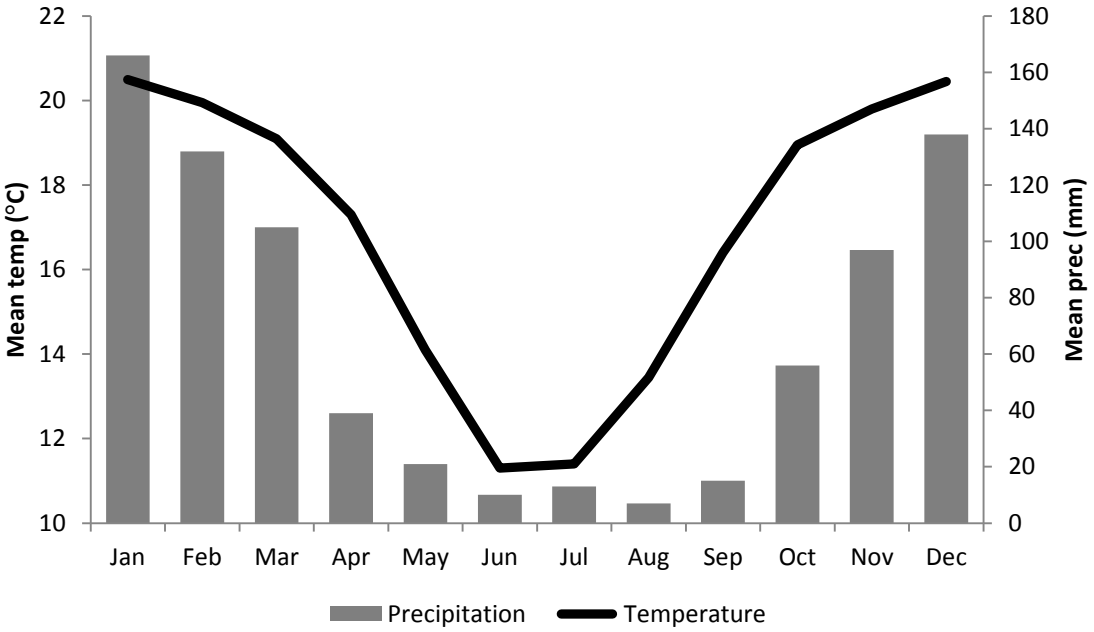

Figure 2.3 Mean monthly precipitation and temperature from 1950-2000 at Lajuma's location. Data extracted from data available at http://www.worldclim.org (Hijmans et al. 2005).

2.2.4 Flora

The main biomes present in the Soutpansberg area are forest, savannah and grassland plus some azonal plant communities. However, substantial local variation in abiotic factors such as elevation and water availability result in various microclimates which are able to support a substantial diversity of both flora and fauna (Brock et al. 2003, Willems 2007). The Soutpansberg area contains 2693 plant species (including 594 tree taxa), including 24 endemics and compromising 1066 genera and 240 families (Hahn 2006). The most unusual characteristics of the Soutpansberg flora are the number of succulents (10% of all taxa) and the number of plants dependent upon mist precipitation (Willems 2007).

There are three main local vegetation types: northern mistbelt forest, Soutpansberg mountain bushveld and Soutpansberg summit sourveld (Musina & Rutherford 2006).

Northern mistbelt forest is distributed across much of the Limpopo and Mpumalanga provinces and into Swaziland, and is composed of tall, evergreen afrotemperate mistbelt forest which is typically species rich. Soutpansberg mountain bushveld is found only in the Soutpansberg Mountain Range and surrounding areas and is mainly composed of thickets, savannah sandveld and arid mountain bushveld. Soutpansberg summit sourveld tends to only be found in areas above 1200m in the Limpopo region (Musina & Rutherford 2006). The forest type is a mixture of grasslands and bush clumps with interspersed rocky outcrops.

2.2.5 Fauna

The Soutpansberg area is home to 59.9% (145) of mammal species found in South Africa (Gaigher & Stuart 2003), 76% (510) of non-oceanic bird species (Tarboton et al. 2003) and 36% (116) of reptile species (Gaigher 2003). Also residing in the area are 28% (44) of all freshwater fish species found in southern Africa (Fouche & Gaigher 2003); mainly due to the presence of South Africa's only freshwater lake, Lake Fundudzi. There has yet to be a comprehensive count of the spider species in the Soutpansberg area, however, in a 50km^2 around Lajuma 337 species have been recorded, which compared to Kruger (139 species) confirms Lajuma as a spider diversity hotspot (VBR 2008). All of these statistics illustrate the diversity present in the Soutpansberg area and therefore its ecological importance.

All five southern-African non-human primates are resident in abundance at Lajuma: the vervet monkey, samango monkey, chacma baboon, thick-tailed galago (*Otolemur crassicaudatus*) and southern lesser bushbaby (*Galago moholi*). Species often seen feeding alongside the samango group, without any agonistic interactions, were vervet monkeys, baboons, rock hyrax, crested guineafowl (*Guttera pucherani*), bushbuck (*Tragelaphus scriptus*) and red duiker (*Cephalophus natalensis*). The samangos were also occasionally observed reacting to these species' alarm calls. Throughout Africa samango monkeys' main predators are leopards (Hayward et al. 2006), eagles (Skorupa 1989, Struhsaker & Leakey 1990), snakes (Foerster 2008) and chimpanzees

(Wrangham et al. 1990, Mitani & Watts 1999). Likely predators at Lajuma therefore include the leopard, crowned eagle (*Stephanoaetus coronatus*), African black eagle and the African rock python (*Python sebae*). Other possible predators present include the caracal (*Felis caracal*), serval (*Leptailurus serval*), African wildcat (*Felis silvestris lybica*), brown hyaena (*Hyaena brunnea*), honey badger (*Mellivora capensis*), Verreuax's eagle owl (*Bubo lacteus*) and members of the Viverridae. The most dangerous venomous snakes on site are black mamba (*Dendroaspis polylepis*), Mozambique spitting cobra (*Naja mossambica*) and the puff adder (*Bitis arientanus*). Although too small to be considered true predators of the samangos, these snakes still elicited alarm calls from the group when encountered, indicating perceived risk. One instance of predation on a samango juvenile by an eagle was observed during my residency on site; based on the location of the event it was likely a black eagle (Gaigher, S., pers. comm.). Chacma baboons are known regular predators of the vervet monkeys at Lajuma (Willems 2007); however, very little aggression from baboons towards samangos has ever been observed on site and there has never been any evidence of predation (Gaigher, I.G., pers. comm. & my pers. obs.). The samangos did not seem to treat the baboons as a threat and the two species often fed in the same tree.

2.3 Study group

The sub-species of samango monkeys found at Lajuma is *C. m. erythrarchus* (Lawes 1990). This is the second most southerly of the *C. mitis* subspecies, ranging from the Mlanje Plateau in southern Malawi, through Zimbabwe, much of Mozambique, to the Limpopo Province and northern KwaZulu-Natal in South Africa (Lawes 1990) (Figure 2.4). They are a light grey colour, often with a patch of red fur under the base of the tail (Groves 2001, pers. obs.).

At Lajuma there are two large fully habituated samango groups. Upon first arrival in October 2009, estimates put one group at approximately 50 individuals and the other

40. Samangos are renowned as being extremely difficult to individually identify (Lawes, M. J., pers. comm.), so preliminary work began with the smaller group to hopefully increase the chance of identifying a considerable proportion of the adults. Juvenile/infant identification was almost impossible and therefore abandoned as an option early on. Mothers carrying infants were especially hard to identify due to their wariness of my presence. By December 2009, 10 of the 15 adults (including the male) were identified. Therefore, whilst there are some unidentified adult females not present in collected focal data, the identified majority should give an accurate representation of the group. Following this preliminary work, it was decided that data collection would continue using the smaller habituated group. Data collection began in January 2010 and was completed at the end of December 2010, representing 12 complete months. Due to low habitat visibility and a large group spread it was extremely difficult to complete accurate censuses of the study group; a number of counts were attempted but only two complete counts were achieved during the study period (see Table 2.3).

Table 2.3 Group compositions from two complete censuses of the focal group.

Date	Adult male	Adult females	Juveniles	Infants	Unsure	Overall
28/12/2009	1	14	17	7	0	39
13/05/2010	1	10	19	7	3	40

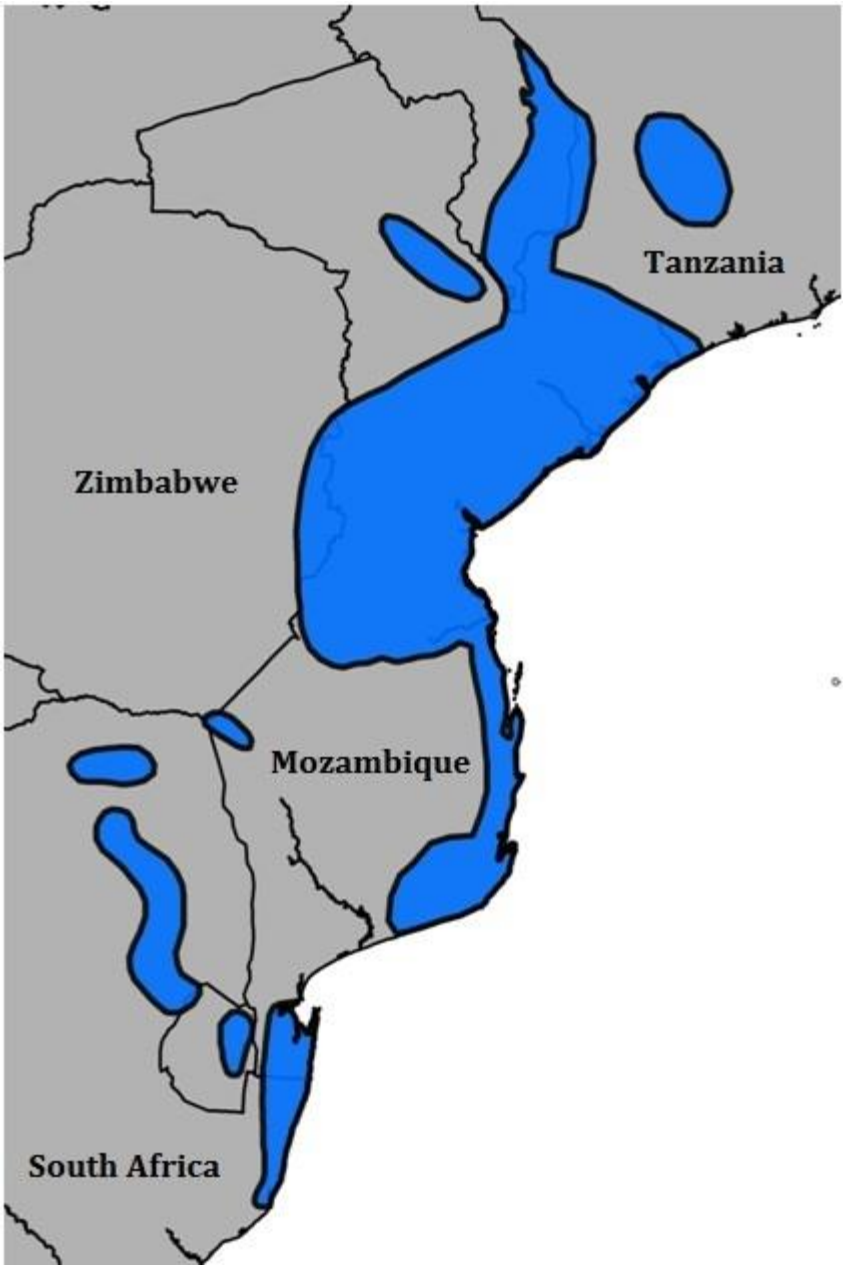

Figure 2.4 Distribution of *C. m. erythrarchus* subspecies (blue) in south-east Africa.

2.4 Data collection

2.4.1 Hardware and software

Data were collected using a palmtop (Sony Clie SL-10) with behavioural data collection software (Pendragon Forms 4.0; Pendragon Software, Libertyville, Illionois, USA and Elan 2.0.1; ©Dennis Sanders). GPS data were collected utilising two units, a Garmin GPS 60CSX and a Garmin GPS 60 (Garmin, Olathe, Kansas, USA). Supplementary data were recorded in paper notebooks.

All GPS data were downloaded onto a laptop using Garmin Mapsource (Version 6, Garmin Ltd) and converted to GIS compatible files utilising DNR Garmin (Version 5.4.0, Minnesota Department of Natural Resources). GIS work was completed using ArcGIS (Versions 9&10, ESRI 2011, Environmental Systems Research Institute, California). An ortho-rectified Quickbird satellite image of the area was utilised as a GIS basemap. All locational data collected were projected into the Universal Transverse Mercator coordinate system (WGS 1984, zone 35s). All output raster files in GIS were set to a cell size of 3m to match GPS accuracy.

2.4.2 Atmospheric monitoring

During the data collection period the on-site weather station was annexed by a colony of ants, damaging the equipment and causing new data to become unreliable. Unfortunately this meant that all on-site weather data collected had to be disregarded. The nearest alternative weather station was at the Mara Research Station (29°34’12’’E, 23°9’0’’S) approximately 18km south-east of the study site and approximately 300m lower in elevation. From this weather station mean monthly rainfall and temperature measurements were extracted (Figure 2.5). Day lengths were calculated using a Garmin GPS 60CSX, which gives accurate data on dawn and dusk times. These times were obtained for each follow day and mean monthly day length was calculated (Figure 2.5).

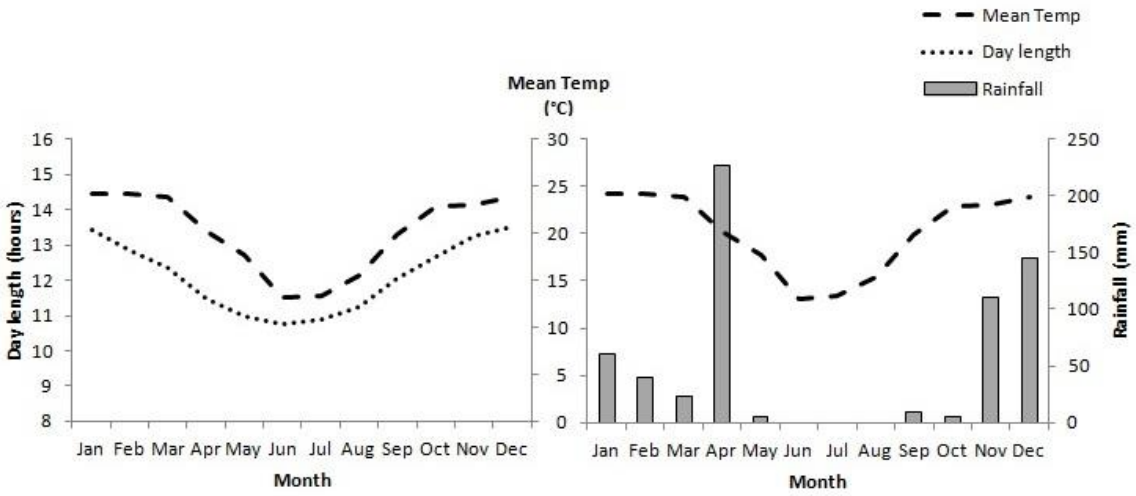

Figure 2.5 Weather and day length patterns for the year 2010. Rainfall and temperature recordings collected at Mara Research Station (29°34'12''E, 23°9'0''S) with day length periods for Lajuma Research Centre (29°26'05''E, 23°02'23''S). Variables presented: mean temperature (Mean Temp), total rainfall (Rainfall) and day length.

2.4.3 Habitat map

Based on various soil types, altitudes, aspects, slopes and water availability it would be possible to describe an endless number of different vegetation types in the Lajuma area. By consulting literature (Edwards 1983, Musina & Rutherford 2006, Mostert 2007) and in conversation with Prof Ian Gaigher a total of 11 basic habitat types were defined in and around the monkey home range, as follows:

1. *Tall forest*

Semi-deciduous forest with >80% canopy cover and the remainder consisting of rocky areas with no grass cover. Mean canopy height is >10m up to a maximum height of 20m. Mostly evergreen with common tree species including *Drypetes gerrardii, Xymalos monospora* and *Rhus chirindensis*.

2. *Short forest*

Similar to tall forest with mean height of trees <10m. May include patches of bushveld, due to boundaries being often extremely difficult to distinguish. Common tree species include *Mimusops zeyheri*, *Acacia karroo* and *Gymnosporia harveyana*.

3. Riverine forest

Tall forest around water courses. Characterised by the presence of the water-berry tree (*Syzygium cordatum*).

4. *Open mountain bushveld*

<20% rocky areas, <50% canopy cover with grasses present and characterised by sandy and/or loamy soils.

5. *Closed mountain bushveld*

<20% rocky areas with 50-80% canopy cover and grasses present.

6. *Open rocky bushveld*

>20% area consisting of rock outcrops and with <50% canopy cover.

7. *Closed rocky bushveld*

>20% rock outcrops with 50-80% canopy cover

All of the bushveld habitat types were dominated by thicket species such as *Acacia ataxacantha* and *Acacia karroo*.

8. *Mountain grassland*

<5% trees and <20% rock outcrops, dominated by grass species.

9. *Wetland*

Open (<50% canopy cover). Characterised by swampy, organic rich soils with moist grass and sedge species

10. *Sandforest*

Forest islands in areas of mountain grassland, also known as woody patches. Usually associated with termite activity

11. *Exotic forest*

Areas of planted trees, usually eucalyptus spp.

The map was made by moving within the areas and categorising the areas based on the above descriptions. GPS data were then uploaded to GIS. Only areas >500m^2 were included in the map. See Figure 2.6 for the habitat map in the surrounding area of the focal group home range.

2.4.4 Vegetation sampling

Plants account for the majority of the year-round diet in all samango monkey long-term studies (Cords 1987, Lawes 1991, Kaplin 2001). To fully understand the movements of the samango monkeys it was important to understand food availability around their home range. To accomplish this, a list of 24 potentially important plant species was constructed using preliminary observations; the findings of a project conducted on site on the subject (Heikamp 2008) and in discussion with Prof Ian Gaigher (Table 2.4).

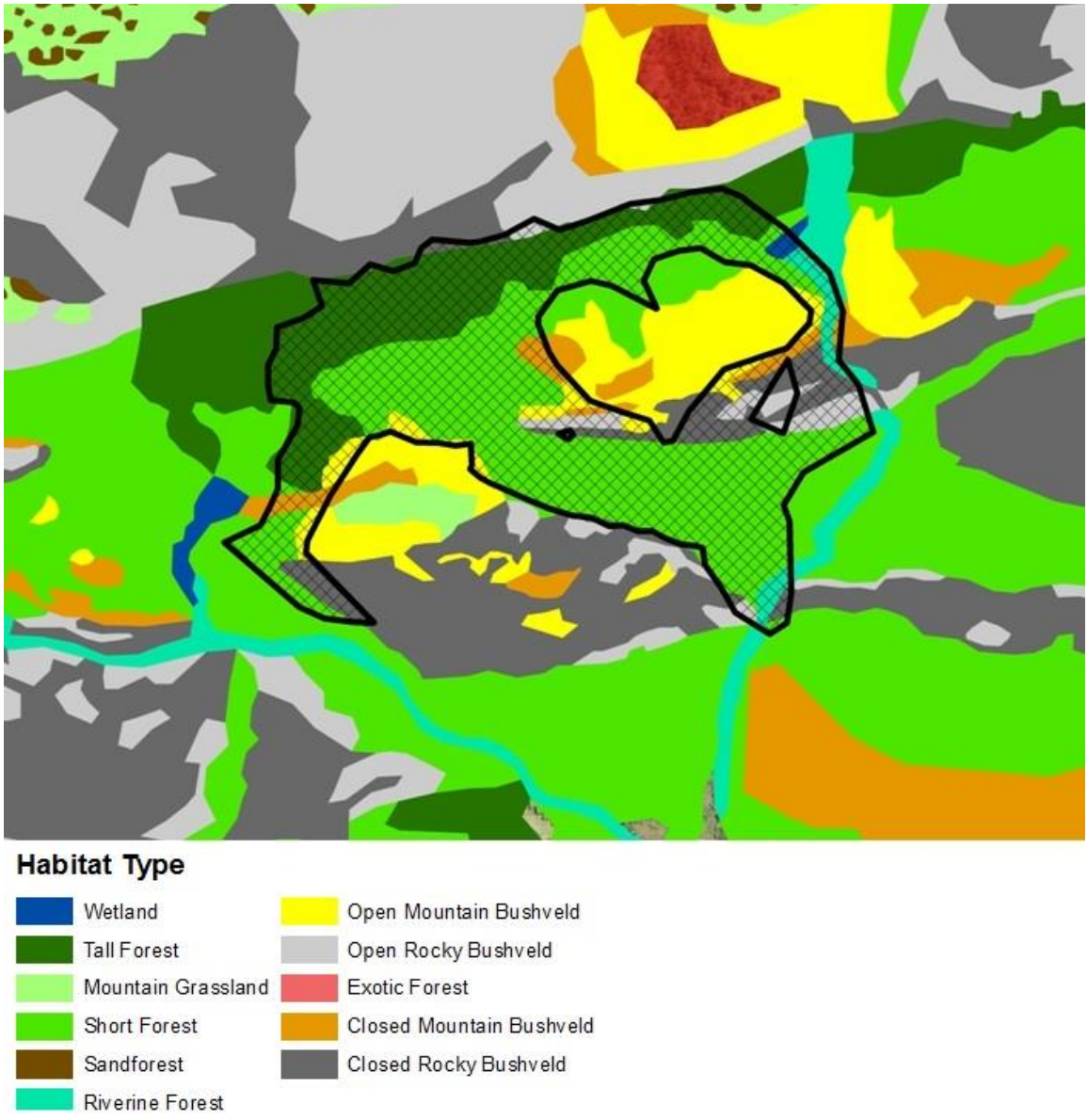

Figure 2.6 Map of habitat types in a section of Lajuma. Hatched area indicates home range of the study group of samangos in 2010.

Table 2.4 List of 24 plant species considered potential food sources for *C. mitis* on site.

Common name	Scientific name
Flame thorn	*Acacia ataxacantha*
Sweet thorn	*Acacia karroo*
Forest num-num	*Carissa bispinosa*
Simple-spined num-num	*Carissa edulis*
White stinkwood	*Celtis Africana*
Forest fever-berry	*Croton sylvaticus*
Wild apricot	*Dovyalis zeyheri*
Forest ironplum	*Drypetes gerrardi*
Cape ash	*Ekebergia capensis*
Stem-fruit	*Englerophytum magalismontanum*
Twin red-berry	*Erythrococca trychogyne*
Common wild-fig	*Ficus burkei*
Forest fig	*Ficus craterostoma*
Broom-cluster fig	*Ficus sur*
Black-forest spike-thorn	*Gymnosporia harveyana*
Wild olive	*Olea europaea*
Quinine tree	*Rauvolfia caffra*
Red currant	*Rhus chirindensis*
Crow berry	*Rhus pentheri*
Cape graph	*Rhoicissus tomentosa*
Water-berry	*Syzygium cordatum*
Forest mahogany	*Trychillia dregeana*
Lemon wood	*Xymalos monospora*
Buffalo thorn	*Ziziphus mucronata*

Phenological transects

To monitor the developmental stages and counts of plant parts of the species selected, phenological transects were set-up. 10 mature individuals, of various sizes, of each species were selected and tagged. The selection was spread throughout the monkey home range as evenly as possible (Figure 2.7). For each tree, data on slope and aspect of ground were collected and then monthly data collected were: height of tree; crown diameter at widest point; crown diameter perpendicular to widest point; number of leaves; percentage mature leaves; number of flowers; number of fruits; percentage ripeness (underripe/ripe/overripe). These data allows the accurate understanding of the developmental stage of important plant species, particularly fruiting period.

Quadrat sampling

Quadrat sampling was used to calculate food availability in the home range. Each month, 125, 5m x 5m quadrats were randomly selected throughout the monkey home range using the ArcGIS add-on Hawth's Tools (Beyer 2004). These were then downloaded to a GPS (Garmin GPS 60) (Figure 2.7). Due to difficulty with the terrain not all these quadrats could be completed, so a minimum of 100 were sampled per month. Once located a pole was used to mark the north-west corner of the quadrat. In each quadrat data recorded were: aspect; slope; percentage rockiness/herb cover/grass cover and number of saplings. Only trees with a circumference ≥0.1m at a height of 1m were included; these were identified and then measurements on height; diameter at widest point and crown diameter perpendicular to widest point were recorded.

To account for overlapping of quadrats and to create maps of the spatial distribution of components of the vegetative structure of the area, kriging was used. Kriging is a geostatistical interpolation technique, utilising observed data points to estimate values for unobserved locations (Cressie 1990). For each estimation a search radius has to be defined, detailing the number of observed data points to be used to make the calculation. For each interpolation, to minimise error within the estimations, the

search radius was selected as the number of points achieving the minimum root mean squared error (Salih et al. 2002).

2.4.5 Visibility

Every two months during quadrat sampling, visibility measurements were recorded (Figure 2.7). At each quadrat, the northwest point of the quadrat was designated the viewing point, where a person would stand. Another person would hold a 0.8 x 0.8m grid with 0.1 x 0.1m cells, 5m directly north of this point, with the top of the grid at a height of 2m. The person standing at the northwest corner of the quadrat would make an estimate of what proportion of the grid was visible. This was repeated at the other three cardinal points. By combining these a mean lower canopy visibility measurement from that area could be obtained.

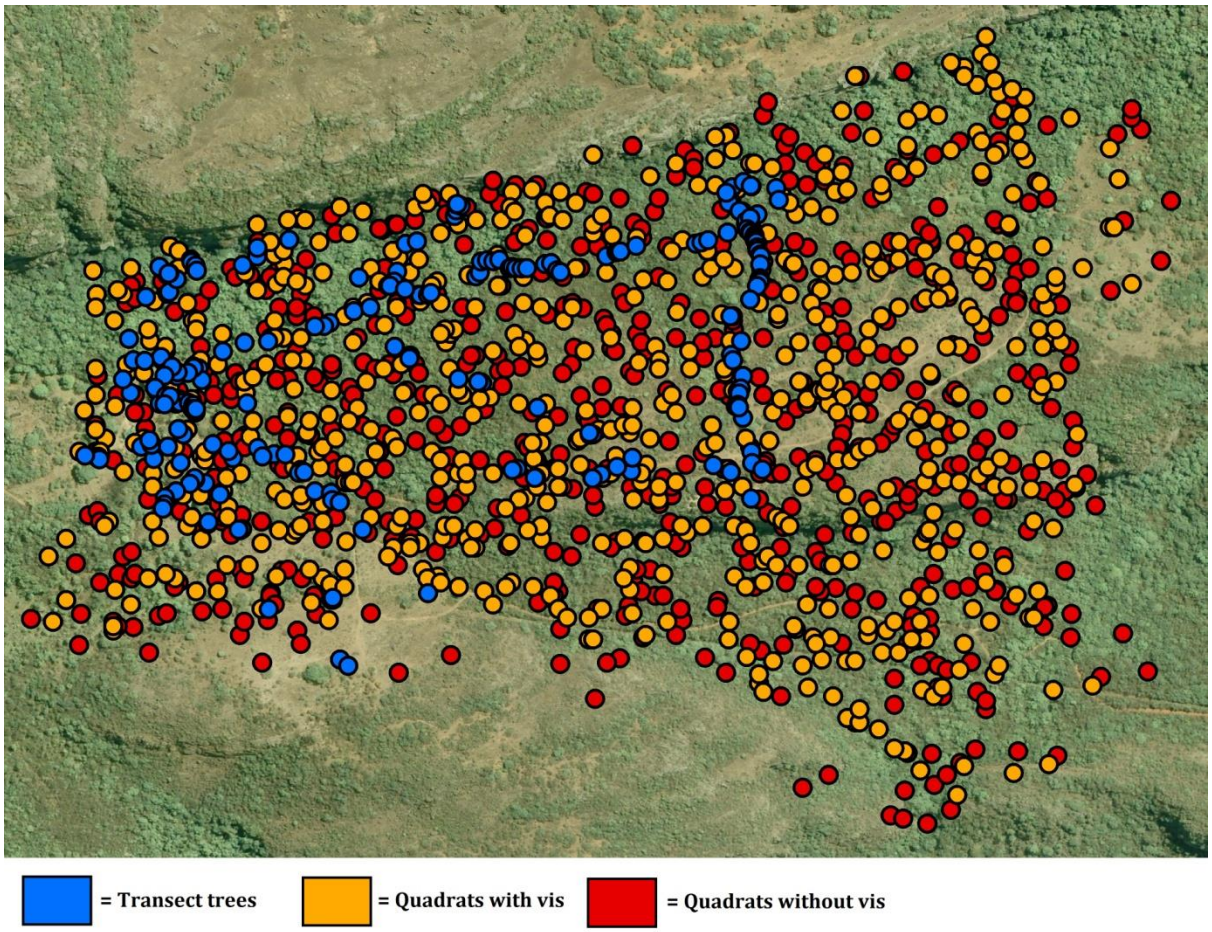

Figure 2.7 Locations of quadrats with (yellow markers) or without visibility (red markers) measurements and locations of phenological transect trees (blue markers).

2.4.6 Behavioural sampling

The group was followed from dawn to dusk for eight days per month. With days ranging from 11h 18m to 13h 32m, total contact hours equated to 1292 hours. A complete follow day involved not losing audiovisual contact with the focal group for more than a total of 60 minutes. During these follow days a variety of different behavioural sampling methods were employed.

GPS Recordings

A Garmin GPS 60CSX can record location constantly to an accuracy of approximately 3m using its tracking function. Every few seconds the unit takes a recording including location, altitude and time, then all the data can be later downloaded to a PC. As long as behavioural recordings included a time measurement they could be coupled to a GPS location at a later date.

Instantaneous scan sampling

Scan sampling involved scanning the behaviour of the entire group at predetermined regular intervals (Simpson & Simpson 1977). I scanned the group throughout the day every 30 minutes on the hour and half hour. These periods would last a maximum of five minutes during which as many adults/juveniles as possible were sampled. Each instantaneous sample included the following information:

i) Time.
ii) ID of the individual.
iii) Activity state – Feeding, moving, resting, eating from cheek pouches, socialising or unknown (Table 2.5).
iv) Vigilance – Social vigilance (including the ID of the individual being looked at), looking up, looking down, scanning horizontally, looking at the observer, no vigilance or face obscured (Table 2.6).
v) Position – In the centre or edge of the group.
vi) Height – Height from the ground in metres.
vii) Number of adults/juveniles within 5m of the focal individual.
viii) I.D. of nearest adult or juvenile.
ix) Any infants within 5m (yes/no).
x) Carrying an infant (yes/no).

Although it could not be eradicated, bias was reduced by moving around the group in between samples to try and ensure different individuals were sampled each time. On

average approximately 65 instantaneous samples a day were recorded, giving a total of 6561 samples throughout the course of data collection.

Table 2.5 Activity types. Once an activity state was selected there were further categories to assess the behaviours exhibited.

Activity State	Definition	Further Recordings 1	Further Recordings 2
Feeding	Stationary consuming or searching for food.	Searching, eating	Type/species of food being eating
Moving	Movement, whilst not engaged in any of the other activity types.	Walking, running, climbing	Speed (slow, normal, fast)
Resting	Staying stationary, whilst not engaged in any of the other activity types.	Autogrooming, sitting, lying, standing quadrapedally/bipedally	Branch, rock, ground
Eating from cheek pouches	Chewing food stored in cheek pouches.	Sitting, lying, standing quadrapedally/bipedally	Branch, rock, ground
Social	Any activity involving another individual.	Allogrooming, playing, fighting, fornicating	ID of the animal/s involved
Unknown	Focal individual obscured		

Table 2.6 Vigilance categories used in sampling.

Vigilance category	Description
Social	Looking towards group members or at a specific individual
Look-up	Looking towards the sky for an aerial threat
Look-down	Looking towards the ground for a terrestrial threat
Scanning	Scanning horizontally
Observer	Looking directly at the observer
No Vigilance	Not being vigilant
Out of Sight	Face obscured

Focal sampling

Focal samples were obtained in order to obtain detailed information on specific individuals (Altmann 1974a) and allow for a relatively unbiased view of the behaviour of the adults in the group. Each day was split into four quarters of equal length. Each identified adult individual was observed for a nine minute focal sample once in each quarter per month. In each nine minute period, up to 10 instantaneous samples were recorded, with a minimum of seven samples. The following data were recorded on each occasion: activity state (Table 2.5); vigilance (Table 2.6); position; height; number of individuals within 5m; nearest individual; infants within 5m (yes/no); carrying an infant (yes/no).

Due to difficulty with identification and individuals leaving the group or dying, not all individuals could be sampled throughout the entire study period, see Table 2.7 for the total data collection periods for the focal animals and Table 2.8 for the number of instantaneous point samples available per individual per month. Focal samples accumulated to an overall total of 3644 instantaneous samples.

Table 2.7 Periods of focal data collection for individually identified focal individuals.

Sample period (months)	12	11	10	9
Number of individuals	5	1	1	1

Table 2.8 Breakdown of focal sampling information.

Monthly follow days	Daily quarters	Length of focal sample (mins)	Number of point samples per focal sample	Number of focal samples per individual per quarter	Number of focal samples per individual per month	Max number of instantaneous point samples per individual per month
8	4	9	10	1	4	40

Continuous sampling

The data collection software Elan was used to collect continuous sampling data. Elan displays up to eight options, which when selected store the option chosen along with a time stamp in a separate file. This was ideal for collecting vigilance data in continuous samples as the data could be processed at a later date to indicate glance periods of specific vigilance types.

Similarly to the focal samples mentioned above, each identified adult was sampled four times a month. An individual was continuously observed for a total of 5 minutes (maximum 2 minutes out of sight), recording each time a change in sight direction occurred (see Table 2.6 for definitions). Before each sampling period, information recorded on each individual was: activity; position in group; height; number of

individuals within 5m; any infants within 5m and whether the individual was carrying an infant. If activity type changed during the sample period a note was made immediately using Elan's note function, which applies a time stamp to each note recorded. Any changes in the other categories, such as height, were recorded after each minute of the sample.

Early on in data collection it was realised that keeping track of the activity "moving" was proving too difficult. Therefore, a decision was made to include moving as a vigilance option on the Elan interface. This meant that whist an individual was moving no vigilance data could be recorded. Unfortunately this means that the first month of continuous samples had to be discarded, so only 11 months of continuous sample data were completed. However, between eight focal individuals it was still possible to collect over 1600 minutes of continuous vigilance data.

The other sampling techniques only give information on proportion of time spent vigilant. With them an individual glancing every few seconds may look the same as one glancing every 30 seconds but remaining vigilant for much longer each time. Continuous sampling allows the calculation of glance rate and so allows for much more detailed vigilance data.

Ad libitum recordings

At all times certain recordings were taken *ad libitum*, including: vocalisations; interactions with rival groups; presence of other animals/predators; sexual encounters and dominance behaviours. A time was always recorded alongside a description of the behaviour and could be later tied to a GPS location.

Any adult male vocalisations were counted and recorded. Juvenile and adult female vocalisations were more regular and it was unfeasible to record all of them. Grunts were never recorded and chirps/hacks were recorded at three levels, when in groups of: <10, 10-20 and 20+. An inter-group encounter was defined as visual fixation of the competitor group by at least one member of the study group. Where possible the

individuals involved were recorded. A sexual encounter was defined as copulation between a male and female. If possible the individuals involved were noted. This behaviour was only ever observed between the alpha male and adult females. Agonistic dominance behaviours were very rare, but when they occurred an attempt was made to identify the individuals involved. If any other large animal species were observed either visually or audibly the species was recorded.

2.4.7 Other sampling

Sleeping sites

For each follow day the final GPS recording at dusk was used as the location of the sleeping sites. I attempted to be as close to the centre of the group at that point.

Water locations

Due to the presence of human buildings and above ground water pipes within the home range of the monkeys there was occasional water availability from leaks. If these leaks lasted more than a month its location was recorded. There was also some natural permanent water sources within the home range including a river located at the eastern edge.

2.5 Data analysis and processing

2.5.1 Software

ArcGIS and the add-ons Geospatial Modelling Environment (Version 0.5.5 Beta, Beyer 2011) and Hawth's Tools (Version 3.27, Beyer 2004) were used for modifying spatial data. Data analyses were completed using a combination of SPSS (Version 19, an IBM Company), R (Version 2, R Foundation for Statistical Computing, Vienna), Spatial

Analysis in Macroecology (SAM 4.0, Rangel et al. 2006) and Microsoft Excel (2010 Version, Microsoft, Redmond, Washington).

2.5.2 Food availability

A number of analyses used in the data chapters required food availability to be quantified. To achieve this a measurement of availability of fruit was used, due to samango monkeys' mainly fruigivorous diet (Lawes 1991), and the difficulty in estimating availability of other food sources, such as leaves and animal matter. The calculation of the fruit availability measurement is described below:

Step 1 – Data selection

To calculate fruit availability, the data from the phenological transects and quadrat sampling were used. This calculation was based on availability of fruit from eight of the ten most eaten fruit species during the study period (Table 2.9). *M. zeyheri* was not included in the calculations because of its omission as transect tree species. *O. europaea* was not included due to a lack of fruiting data collected from the transect individuals. The *Ficus* spp. category was used because of the difficulty of differentiating between *F. burkei* and *F. craterostoma* in the behavioural sampling.

Step 2 – Calculation of fruit numbers for phenological transect trees

The first step in the calculation of fruit availability was to use the individuals sampled in the phenological transects to investigate any potential relationships between tree crown diameter and number of fruits counted, for each species. Firstly total number of fruits were summed for each phenological transect individual. Then the two crown diameter measurements from the transect data (widest crown diameter and diameter perpendicular to widest) were averaged to create an average crown diameter measurement for each individual. For each species a linear regression was used to explore the relationship between average crown diameter and total fruit (Table 2.10), with total fruit as the dependent variable. Data for all species but *A. karroo* were normally distributed; for *A. karroo* total fruit was log transformed. *R.*

tomentosa could not be included in this analysis as it is a liana species, making measurement of crown diameters extremely difficult.

Table 2.9 Top ten most consumed fruit species based on data from adult only scan samples. * not included in any fruit availability calculations.

Species	Mean monthly proportion of fruit consumed (%)
Ficus spp.	19.8
A. ataxacantha	13.5
R. tomentosa	13.4
F. sur	11.6
R. chirindensis	10.0
*M. zeyheri**	9.5
E. capensis	5.4
*O. europeaea**	5.1
E. magalismontanum	4.2
A. karroo	1.2

Table 2.10 Results of linear regression analyses with total fruit as response variable and average crown diameter as predictor variable. **A. karroo* total fruit was log transformed prior to analysis to meet normality assumptions.

Species	B (constant)	B (variable)	t	p
*A. karroo**	-.865	.653	4.227	**.002**
A. ataxacantha	-9593.589	3327.974	2.554	**.034**
E. capensis	-55714.003	10047.131	3.060	**.016**
E. magalismontanum	-646.097	1482.283	1.124	.294
Ficus spp.	-41912.486	9470.824	1.411	.175
F. sur	-6578.576	2469.836	3.816	**.005**
R. chirindensis	3103.451	2139.012	.660	.527

For species which showed significant relationships between average crown diameter and total fruit, equations were created which could be used to predict the total fruit availability for all the individuals identified in the quadrat sampling. The equation utilised was:

Total Fruit = B (constant) x (B (variable) + Average crown diameter)

For the three species which showed no significant relationships in the regression analyses, categorical differences in fruit availability were still discerned based on crown diameter (Figure 2.8) and were used to predict the total fruit of individual trees identified in the quadrat sampling.

For *E. magalismontanum* if average crown diameter was <=2m, this equated to 168 fruits; if it was >2m this equated to 792 fruits. For *Ficus* spp. if average crown diameter was <10m this equated to 36257 fruits; if it was >=10m this equated to 77290 fruits. For *R. chirindensis* if average crown diameter was <5m this equated to

4236 fruits; if it was >=5m this equated to 28700 fruits. Finally, for *R. tomentosa* an average of 205 fruits per individual plant was calculated.

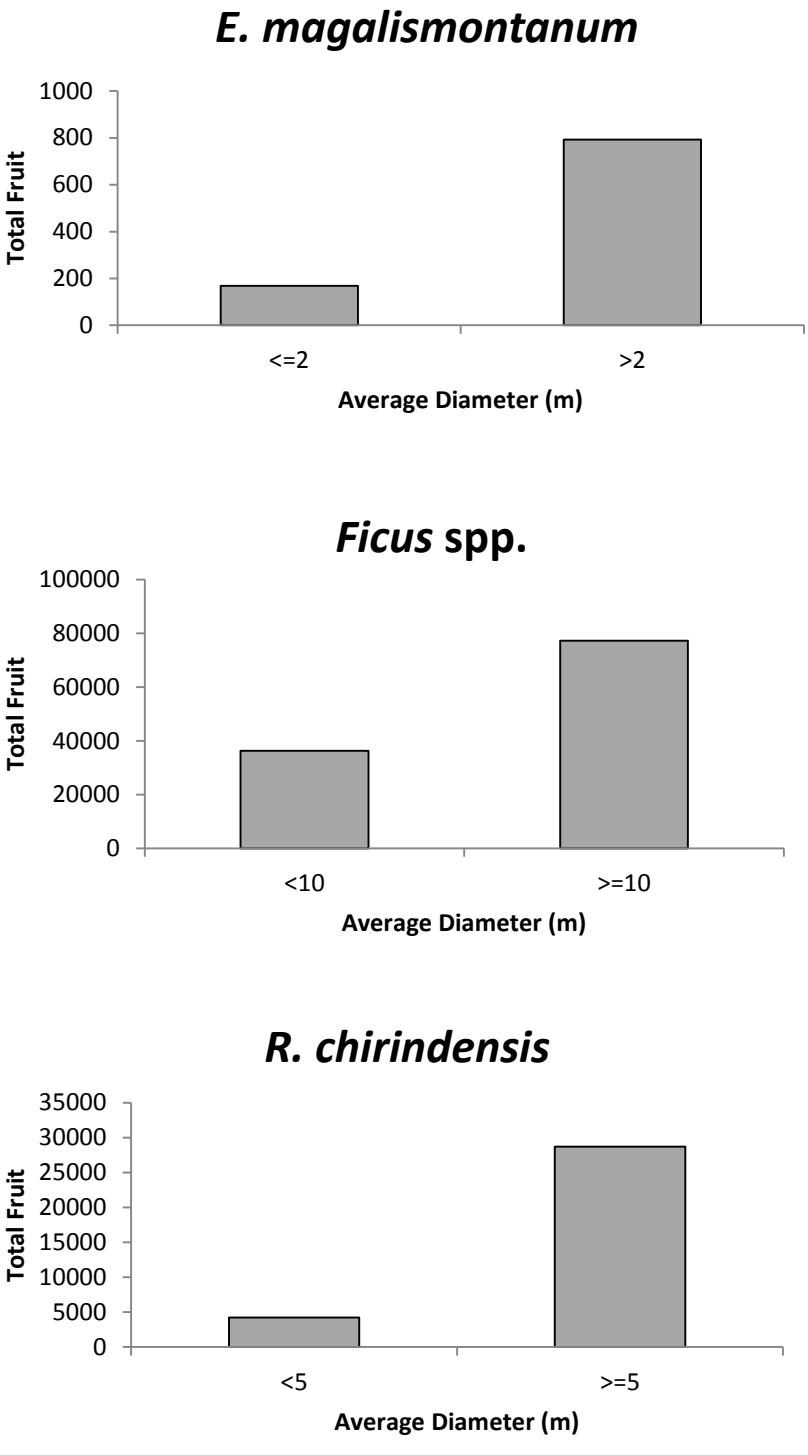

Figure 2.8 Charts detailing average total fruit for three tree species monitored in phenological transects.

Step 3 – Conversion to all quadrat sampled trees

The equations and relationships generated in Step 2 allowed for the estimation of annual fruit availability for any individual of the eight tree species within the quadrat sampling. Therefore to calculate total fruit availability throughout the monkeys' home range the fruit availability of every individual (of the eight species) recorded in the quadrat sampling was calculated. From this a total fruit availability for each quadrat sampled was calculated.

Step 4 – Conversion to fruit sizes

Different species have different fruit sizes, so using total number of fruits could create an inaccurate representation of fruit availability. Fruit volume was thus used as the unit of measurement for fruit availability. Fruit numbers were converted to total fruit size based on volume measurements in Coates-Palgrave (1996) (Table 2.11; *Acacia* pods were given a nominal thickness of 1mm). This conversion removed the potential inaccuracy caused by, for example, *Rhus chirindensis* having much smaller fruits than *Ficus sur.*

Table 2.11 Fruit sizes used for fruit availability calculations. All fruit size data taken from Coates-Palgrave (1996). *Acacia* pods given a nominal thickness of 1mm.

Species	Fruit size (cm^3)
A. karroo	1.6
A. ataxacantha	4.8
E. capensis	1.77
E. magalismontanum	2.81
Ficus spp.	.32
F. sur	22.45
R. chirindensis	.065
R. tomentosa	4.19

Step 5 – Monthly fruit availability

Using known monthly fruiting variation of the phenological transect individuals the monthly fruit availability for each quadrat sampled was also calculated.

2.5.3 Home range

Local Convex Hulls (LoCoH) analysis is a recently developed method (Getz & Wilmers 2004, Getz et al. 2007) used for the calculation of home ranges and intensity of space use. LoCoH analysis is essentially a nonparametric kernel density estimation which constructs convex hulls around each data point and uses these to determine utilisation distribution (Getz et al. 2007). LoCoH has been shown to have superior convergence properties, to be better at defining hard boundaries such as cliffs and rivers and to be better coping with clumping/repeat data points than kernel density estimation (Getz & Wilmers 2004, Hemson et al. 2005, Ryan et al. 2006, Getz et al. 2007). The adaptive LoCoH method is one of three variations of LoCoH analysis, and enables smaller convex hulls to arise in higher usage areas, allowing more detailed information in areas of clumped data (Getz et al. 2007). Adaptive LoCoH was the method used for all calculations of home range. For adaptive LoCoH analysis it is suggested that the widest point between two locations is used as the value *a* in order to ensure the correct formation of the 100% isopleths (Getz et al. 2007). The calculations for the analysis were achieved using R (Version 2.13 The R Foundation for Statistical Computing 2011), generating isopleths in 1% divisions. This was then uploaded to ArcGIS for further manipulation and presentation.

2.5.4 Statistics

As a general rule assumptions of all statistical methods were assessed prior to analysis. All the analyses and models are described in detail within the data chapters where they have been utilised.

Chapter 3

Seasonal Variation in Basic Ecology

3.1 Introduction

To survive and reproduce an animal must adapt its behaviour to the environmental conditions it experiences (Krebs & Davies 1993). This is often expressed in its ability to efficiently control its net energy intake; however, there are a number of factors which potentially disrupt an animal's ability to achieve this. One such factor is climatic variation, both spatial and temporal, which can have important effects on habitat structure, primary productivity and eventually food availability (Mohamed et al. 2004). By studying populations at the edge of a species' distribution it is possible to investigate the extent they are able to adapt their behaviour to survive, when at the limits of their ecological tolerance (Sexton et al. 2009). As an isolated population near the southerly limit of the species range, samango monkeys resident in the Soutpansberg Mountains, South Africa provide an excellent study model in this regard.

One of the most important drivers of climatic variation around the globe is the effect from the seasons, a result of the annual revolution of the Earth around the Sun and the tilt of the Earth on its axis (Khavrus & Shelevytsky 2010). Many animals have to continually adapt their behaviour to the changing conditions associated with the seasonal variation they encounter (Wolda 1988, Williams et al. 2001, Zhou et al. 2007). The investigation of the effects of seasonality in a primate study population is best achieved through long-term observational studies (Brockman & van Schaik 2005). These allow the observation of seasonal trends in factors such as ranging behaviour, activity budgets and diet composition. Therefore, the aim of this study is

to investigate the effect of seasonally variable environmental conditions on the behavioural ecology of a group of wild samango monkeys.

3.1.1 Ranging

Seasonal fluctuations in certain resources, particularly food availability, may cause primate groups to utilise their home ranges in different ways. For example, in seasons of reduced food availability primates may respond by travelling less and being less selective about the items they eat. In the winter months Japanese macaques respond to the conditions by reducing distance travelled to reduce energy expenditure (Hanya 2004). A similar pattern has been observed in capped langurs (*Trachypithecus pileatus*) (Stanford 1991) and chimpanzees (Doran 1997). Alternatively, some primates may travel further to find rarer, higher quality food items (Waser 1977, Volampeno et al. 2011). A study on Sichuan snub-nosed monkeys observed that during the warm, wet summer when fruit availability was higher, range size and day journey length increased significantly (Li et al. 2010). The suggested reason for this pattern was the relatively sparse distribution of an important fruiting tree to the monkeys.

In a study on samango monkeys in the Kibale Forest, Uganda, there were two peaks of day journey length within the study group which occurred in June and October (Rudran 1978). These peaks approximately coincided with the two annual rainy seasons in Uganda, which are usually around April/May and October/November (Hijmans et al. 2005). There was also an observed peak of home range size in October, although no second peak was observed earlier in the year. Fruiting information from the Kibale Forest indicates fruit production often peaks just after the rainy seasons especially around May (Chapman et al. 1999). This suggests a potential positive correlation between day journey length and fruit availability for samango monkeys at that study site. Although this samango monkey study indicated a potential seasonal pattern between food availability and ranging, a different long term study was unable to find any significant relationships between the two (Cords 1987).

For an arboreal monkey species, such as samangos, there is another element of range use which has the potential to vary seasonally, and that is time spent on the ground (terrestriality). Many arboreal primates avoid spending much time on or near the ground mainly due to the associated higher risk of predation from terrestrial predators (Isbell 1994, Emerson et al. 2011). Therefore, it is possible that an arboreal species may descend to the ground for food at times of lower food availability within the upper canopy. A study on Sichuan snub-nosed monkeys observed a significant increase in terrestriality during the summer months, which are associated with the availability of the herb heracleum (*Heracleum hemsleyanum*) which is known to be an important source of protein for that population (Li 2007).

An important effect of ranging variation might be the associated effect on the amount of time an individual can attribute to certain activities, also known as their activity budget. If an individual uses more of their range, therefore spending more time moving, they may have less time available for other activities such as resting or socialising (Gursky 2000). Therefore, it is important to investigate the potential effects seasonality can have on the activity budgets in primates.

3.1.2 Activity budgets

In seasons with reduced food availability primates may spend more time searching for food (Garber 1993, Gursky 2000), spend more time feeding on lower quality foods (Doran 1997, Hill 1997, Guo et al. 2007) or spend more time resting in order to reduce energy expenditure (Chaves et al. 2011). Alternatively, an individual may be forced to increase time feeding at times of high food availability, to increase energy stores for times of lower availability. An example of this is Peruvian spider monkeys (*Ateles chamek*), which have been observed increasing feeding time during the wet season in order to store surplus fat for the upcoming dry season (Felton et al. 2009).

The study of the effects of season on activity budget may help us explain species distributions. For any species there is a maximum amount of time available to forage

for food (Dunbar 1992, Hill 1999). Therefore, species should only be resident in areas where they are able to allocate enough time to important activities to survive and reproduce successfully (Altmann 1974b). This has important implications for the study population of samango monkeys, which are near the southern limit of the species' distribution (Lawes 1990, Kingdon et al. 2008c) and potentially represent a limit to the ecologically tolerable conditions for the species.

3.1.3 Diet

Many primates vary their diet on a seasonal basis because of the seasonal variation in the availability of certain foodstuffs. For example, many areas experience strong seasonal fluctuations in fruit availability (Conklin-Brittain et al. 1998, Wrangham et al. 1998). Most primates are frugivores and at times of low fruit availability subsidise their diet with different foodstuffs such as leaves (Hladik 1975, Milton 1980, Stanford 1991, Hill 1997), seeds (Galetti & Pedroni 1994, Peres 2000), flowers (Galetti & Pedroni 1994) or invertebrates (Garber 1993). For example, during the dry season, when fleshly fruit availability is low, capuchin monkeys (*Cebus* spp.) will supplement their diet with seeds and flowers (Galetti & Pedroni 1994).

Samango monkeys have special digestive adaptations that allow them to consume relatively large amounts of foliar material, such as long caecums, large numbers of cellulases and large numbers of cellulose digesting bacteria (Bruorton et al. 1991). Based on these adaptations it would be expected that samangos should supplement their diets with leaf material at times of low fruit availability, and this is the pattern observed in previous studies conducted in Uganda (Rudran 1978), Kenya (Cords 1986) and South Africa (Lawes 1991). The majority of samango studies observe a peak in fruit feeding during rainy seasons (Rudran 1978, Lawes 1991), Beeson et al. (1996), although Cords (1986) observed two peaks of fruit consumption, once in the middle of the rainy season and once in the dry season.

3.1.4 Objectives

The overall aim of this study is to investigate the seasonal variation in certain aspects of samango monkey behavioural ecology. This will be achieved through the statistical analysis of long term observational data of a wild group of samangos residing in the Soutpansberg Mountains, South Africa. The predictions of the outcomes of this study are:

1) Home range size and day journey length will increase during the rainy season.
2) Fruit consumption will peak during the rainy season and will be supplemented in the dry season by leaf material.
3) If seasonal variation in leaf/fruit consumption is observed there will be an observable change in time spent feeding due to the fibrous nature of leaves requiring more time for consumption (Milton 1981).

This study presents a detailed investigation into the factors which control seasonal variation in the behavioural ecology of a population at the southerly limit of what is the most southerly ranging African arboreal monkey species (Wolfheim 1982, Kingdon et al. 2008c). This will provide interesting insights into how such a population is forced to adapt behaviourally to survive difficult conditions which few similar species are subject to.

3.2 Methods

3.2.1 Study site

The study site is Lajuma Research Centre, located in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). The local climate is classified as temperate/mesothermal, with cool dry winters from April-September and warm to hot wet summers from October-March (Willems 2007). Substantial local variation in abiotic factors such as elevation and water availability result in various

microclimates which are able to support a substantial diversity of both flora and fauna (Brock et al. 2003, Willems 2007). For a more comprehensive description of the study site see Section 2.2.

3.2.2 Study species

Samango monkeys are primarily frugivorous (Lawes 1991), medium sized, arboreal guenons, which form single-male, multi-female groups with group sizes ranging from 4-65 (Butynski 1990, Beeson et al. 1996, Smith et al. 2008, Houle et al. 2010, Lawes et al. 2011). The species is distributed throughout much of the forested areas of central and east Africa: ranging from Ethiopia in the north of their range, Angola to the west and as far south as the Eastern Cape Province of South Africa. The distribution appears to be limited in the west by the Zaire-Lualaba River system and to the northwest by the Itimbiri River (Colyn 1987, 1988, Wilson & Reeder 1993). This large range means different populations are subject to a large variation in climate types (Hijmans et al. 2005).

3.2.3 Data collection

A habituated samango group of approximately 40 individuals was observed over a 12 months period (Jan-Dec 2010). Data collection consisted of eight successful follow days per (totalling 96 days), with a successful day consisting of following the group from dawn to dusk without losing audiovisual contact for more than a total of 60mins. Study days ranged from approximately 11.5-13.5 hours depending upon season. The behavioural data used in this chapter were obtained from scan sampling (Altmann 1974a) of adult individuals. Scan samples were conducted every 30 minutes; on the hour and half hour. Each scan lasted a maximum of five minutes, during which as many adults/juveniles as possible were sampled. For a more comprehensive description of the methods used see Section 2.4.6.

3.2.4 Climate

Unfortunately during the study period the on-site weather station was damaged and data collected from it were deemed unreliable. Therefore, the temperature and rainfall data were collected from a nearby weather station at the Mara Research Station (29°34'12''E, 23°9'0''S) approximately 18km south-east of the study site and approximately 300m lower in elevation. Day length was calculated using daylight periods extracted from the GPS used in data collection (Garmin GPS C60x), which gives accurate data on dawn and dusk times. These times were obtained for each follow day and mean monthly day length was calculated. The data shows a cold dry winter between the months of May-October and a peak of rainfall in April (Figure 2.5).

3.2.5 Ranging data

When moving, the GPS receiver would record a location every few seconds, which over the 96 follow days yielded more than 120,000 data points. Therefore, for ease of use all GPS locations collected were filtered to 10 minute intervals resulting in 6912 data points.

Home range analysis

Intensity of space use was calculated using adaptive Local Convex Hulls (LoCoH) analysis (Getz & Wilmers 2004, Getz et al. 2007). For a detailed description of the LoCoH method see Section 2.5.3. For adaptive LoCoH analysis it is suggested that the widest point between two locations is used as the value *a* in order to ensure the correct formation of the 100% isopleths (Getz et al. 2007). To calculate the annual home range using the full dataset of 6912 points *a* was set to 1329 metres. Figure 3.1 shows the process of the LoCoH analysis for the annual data, from original GPS locations to the final utilisation distribution. Monthly home ranges were also calculated. Sample sizes of GPS locations and the widest point between locations for each month are given in Table 3.1.

Day Journey Length, Journey Speed and Terrestriality

From the filtered GPS data points used for the home range analyses, annual and monthly mean day journey length were calculated as a measurement of total distance travelled from dawn to dusk. Figures for mean journey speed were also calculated by dividing day journey length by day length. Journey speed was calculated by dividing these figures by day length. Figures for monthly terrestriality were obtained by calculating proportion of time spent on the ground. Annual terrestriality was calculated as mean monthly terrestriality. To permit seasonal analysis monthly data (Table 3.4) were converted into hours per day spent terrestrial by following the methods of Hill et al. (2004).

3.2.6 Activity budgets

Activities were separated into six categories: feeding, resting, socialising (including agonistic interactions), moving, eating from cheek pouches and unknown. Using adult scan sample data mean monthly proportion of time spent in each activity category was calculated. From these data an annual mean was calculated. Similarly to the calculation of time spent terrestrial, in order to compare seasonal variations in activity budgets, each category was converted into hours per day (following Hill et al. 2004).

Table 3.1 Data used for monthly and annual LoCoH analyses. Total home range calculated from these analyses is also presented.

Month	Furthest distance between locations (m)	Number of home range locations	Home range (ha)	Core (50%) home range (ha)
Jan	1169	622	34.3	4.8
Feb	1152	609	26.7	6.3
Mar	888	593	16.2	3.2
Apr	929	552	24.0	5.2
May	937	525	22.4	4.1
Jun	1018	516	25.1	4.7
Jul	1063	509	27.8	4.2
Aug	1073	537	25.1	4.0
Sep	939	573	18.7	3.4
Oct	1168	599	37.1	5.6
Nov	1201	634	29.8	4.5
Dec	1089	643	26.1	5.8
Full Study	1329	6912	54.7	8.3

3.2.7 Diet

Fruit availability

Each month a minimum of 100, 25m^2, randomly placed quadrats were sampled (totalling 1296 throughout the year). Within each quadrat each tree was identified and details such as height and crown size were measured. Coupled with fruiting data from phenological transects an estimate for number of fruits at each quadrat location was calculated. Finally fruit size was accounted for and the final fruit availability figure was calculated (see Section 2.5.2 for a full description of these calculations).

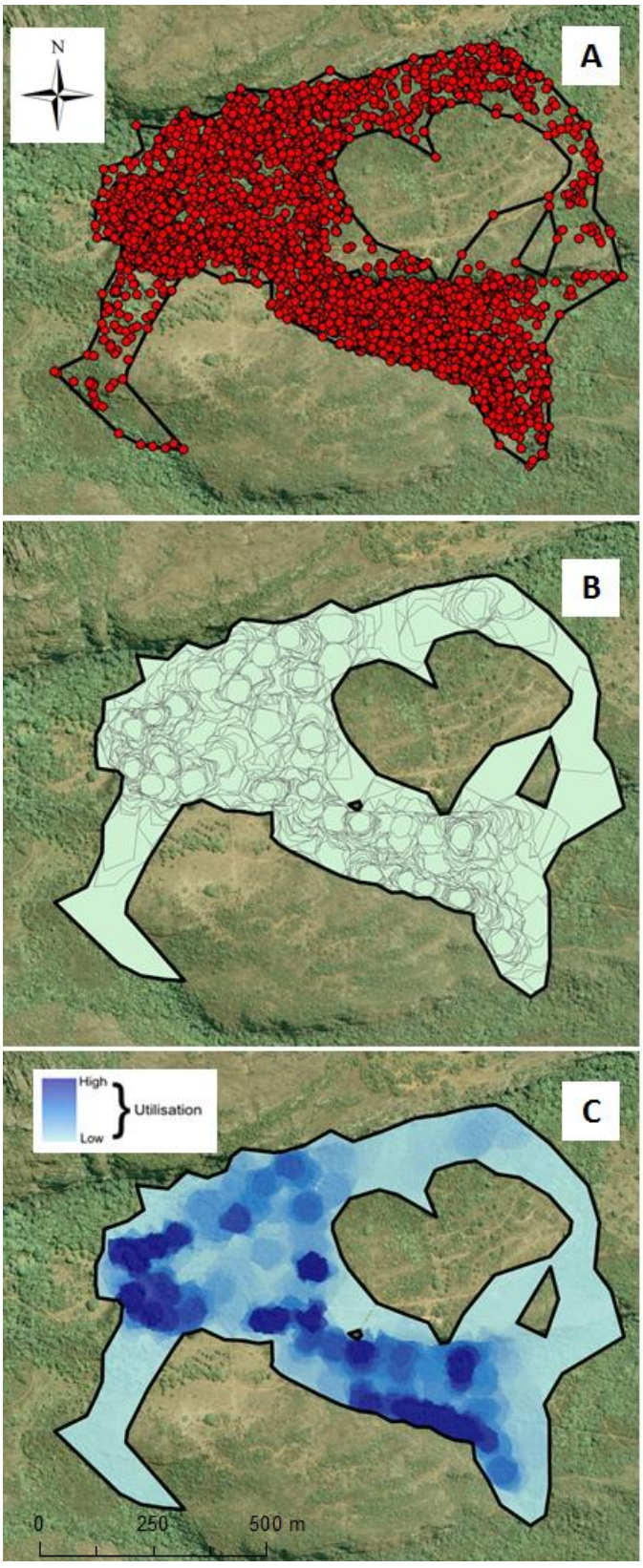

Figure 3.1 LoCoH utilisation distribution analysis for total annual home range (54.7ha).
A= 6912 GPS locations.
B= Convex hulls constructed by the LoCoH analysis.
C= Raster image representing level of utilisation.

Diet composition

Diet composition data were separated into six categories: fruit (including seeds and *Acacia* pods), leaves, flowers, bark, animal matter (invertebrates) and fungi. As with the activity budget calculations annual diet composition was calculated as a mean of monthly figures. In order to compare seasonal data, diet data were converted into hours per day feeding on each category (following Hill et al. 2004).

3.2.8 Statistical analysis

Pearson's linear correlation analyses were used to indicate whether there were any significant relationships between any two variables. Previous studies have highlighted potential problems with multiple tests (Hochberg 1988, Bland & Altman 1995a). However, the analyses were not corrected for the use of multiple tests, because methods, such as Bonferroni corrections, are often discouraged, mostly due to the substantially increased risk of subsequent Type II errors (Perneger 1998, Moran 2003, Nakagawa 2004). All results will therefore only be discussed based on the hypotheses made and the biological merit of the significantly correlated relationships. The effect sizes of all the correlations will also be evaluated, with relationships only accepted as significant if the effect size is substantial (i.e. minimum r =0 .5) (Nakagawa 2004).

To test for normality a Kolmogorov-Smirnoff test was used based on the monthly data. According to the test, all categories except "unknown" from the activity budgets and "animal" and "flower" in the diet composition were normally distributed (Table 3.2). The reason for these results was a lack of data corresponding to these categories and therefore they were not included in any further analyses.

Table 3.2 Kolmogorov-Smirnoff test results for all monthly data categories.

Variable	p	Variable	p	Variable	p
Home range	.599	Resting	.565	Fruit	.863
Journey length	.937	Feeding	.979	Leaves	.691
Journey speed	.982	Moving	.681	Bark	.092
Terrestriality	.989	Socialising	.978	Flowers	**.002**
Rainfall	.514	Pouches	.739	Animal	**.002**
Mean temp	.512	Unknown	**.005**	Fungi	.094
Day length	.955				
Fruit avail	.671				

3.3 Results

3.3.1 Ranging

The home range totalled 54.7ha in size. Previous samango studies range 10-252.75ha (Table 3.3) with a mean of 49ha, indicating that the Lajuma group home range is representative of the species. The core (50%) home range of the study group was 8.3ha. Mean day journey length equated to 1906m (± 276.4). Reported mean day journey lengths range from 594-1406m with an overall mean of 1140m (Table 3.3); again indicating Lajuma samangos are representative of other samango populations. Mean journey speed was 156m/h and terrestriality equated to 22.4% of time.

Table 3.3 Ranging and activity budget data for various study populations of samango monkey. For the purposes of this table, eating from pouches was considered a sub-category of resting. Socialising include aggressive and non-aggressive interactions.

Location	Study length (months)	Group size	Home range (ha)	Day journey length (m)	Feeding %	Resting %	Moving %	Sociali-sing %	Other %	Study
Budongo Forest, Uganda	9	-	10	-	-	-	-	-	-	Fairgrieve & Muhumuza 2003
Ngogo, Kibale Forest Uganda	63	15	252.75	1406	31.7	36.2	24.7	7	0	Butynski 1990
Kanyawara, Kibale Forest, Uganda	63	18.4	32.4	1216	36.2	32.7	19.7	8.3	0	Butynski 1990
Kanyawara, Kibale Forest, Uganda	24	20.8	72.5	-	-	-	-	-	-	Rudran 1978
Kakamega Forest, Kenya	11	43	38	1136	49.4	31.7	15.8	1.2	1.9	Cords 1986/1987
Nyeri Hill, Kenya	8	-	13.73	-	-	-	-	-	-	De Vos & Omar 1971
Muguga Estate, Kenya	8	-	16	-	-	-	-	-	-	De Vos & Omar 1971
Nyungwe Forest, Rwanda	10	29	112.2	1306.7	-	-	-	-	-	Kaplin et al. 1998
Kahuzi-Biega D.R.C	5	10	25	594	32.3	35	23.4	9.2	0	Schlichte 1978
Zomba Plateau, Malawi	12	15	16.5	-	-	-	-	-	-	Beeson et al 1996
Cape Vidal Forest, S.A.	13	32.5	15	-	35.8	22.6	29.4	12	0	Lawes 1991
Cape Vidal Forest, S.A.	26	24	10.92	1183	-	-	-	-	-	Macleod 2000
Lajuma, S.A.	12	40	54.7	1906	28.1	41.5	23.2	7.1	0.1	This study

Table 3.4 displays the correlations between the monthly ranging behaviours and environmental parameters. There is no evidence of relationships between home range size and any climatic variables; however, the seasonal pattern for home range size and fruit availability indicates a potential negative relationship between the two (Figure 3.2, 3.3) and the correlation analysis confirms the relationship is statistically significant. When home range size was at its highest (Oct-Jan) and fruit availability at its lowest, the majority of fruit eaten came from *Rhus chirindensis* and fig species (Table 3.5). Day journey length and journey speed are significantly positively correlated, meaning when the monkeys move further they also are moving quicker. Day journey length correlates positively significantly with mean monthly temperature and day length, indicating that samango monkeys move further on longer days. Day journey length and terrestriality are significantly negatively correlated, indicating that when the monkeys spend more time on the ground they travel shorter distances.

Table 3.4 Results from correlation analysis for ranging behaviours and environmental variables. Variables used: mean monthly temperature (Mean Temp), monthly rainfall (Rain), day length, fruit availability (Fruit Avail), core (50%) home range (Core Home Range), terrestriality (Terrestrial), mean journey speed (Speed), mean day journey length (Journey Length). Significant relationships (p=<.05) are highlighted in bold. r = Pearson's correlation coefficient.

Variable	r / p	Mean Temp	Rain	Day Length	Fruit Avail	Core Home Range	Terrestrial	Speed	Journey Length
Home range	r	.197	.044	.391	-.670	.593	.181	.094	.289
	p	.539	.893	.208	**.017**	**.042**	.574	.772	.362
Day Journey	r	.856	.475	.837	-.140	.564	-.673	.850	
	p	**<.001**	.118	**.001**	.664	.056	**.017**	**<.001**	
Speed	r	.557	.474	.426	.250	.530	-.518		
	p	.060	.120	.167	.434	.076	.085		
Terrestrial	r	-.783	-.453	-.637	-.083	-.202			
	p	**.003**	.140	**.026**	.798	.529			
Core Home Range	r	.365	.413	.411	-.147				
	p	.243	.182	.185	.649				

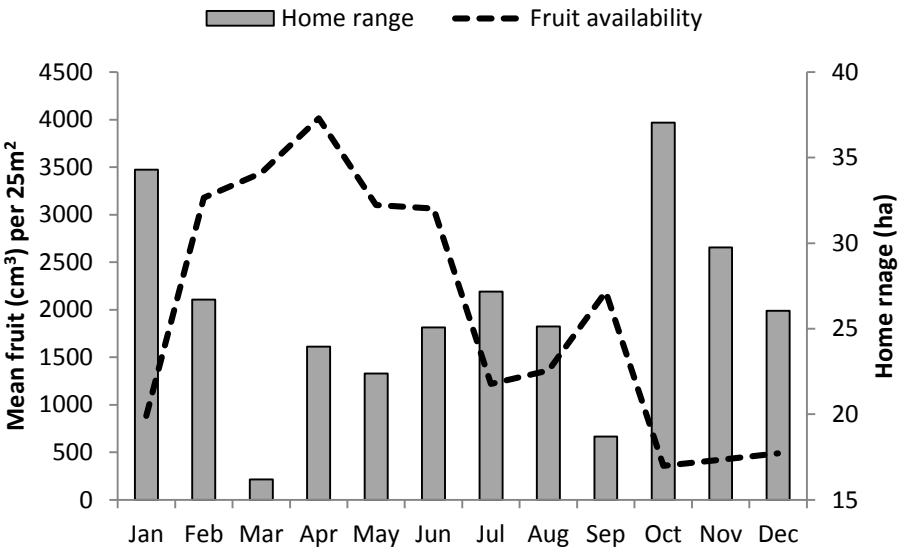

Figure 3.2 Seasonal patterns of mean monthly fruit availability and monthly home range size.

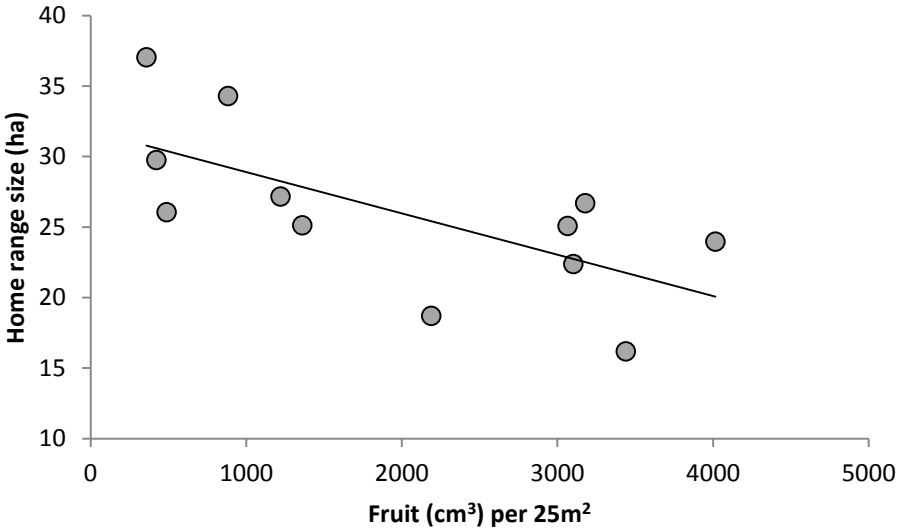

Figure 3.3 Relationship between fruit availability and home range size.

Table 3.5 Mean monthly proportion of time spent feeding on fruit species for the months October-January. Top 5 most eaten fruit species are displayed.

Tree species	% of fruit feeding
Rhus chirindensis	32.6
Ficus spp.	27.7
Ficus sur	13.8
Englerophytum magalismontanum	12.4
Mimusops zeyheri	7.5

3.3.2 Activity budgets

The annual mean activity budget observed within the focal group is similar to that of previous *C. mitis* studies (Table 3.3), although the Lajuma samangos show the lowest proportion of time feeding and highest proportion of time resting than any other previously reported study group. On a month by month basis there appear to be some seasonal variations in the activity budgets of the focal group (Figure 3.4). Most notably time spent feeding observably increased during much of the winter period.

Resting has a significant positive relationship with mean monthly temperature (Table 3.6) and day length; whilst feeding has a significant negative correlation with mean temperature (Figure 3.5), indicating that the monkeys spend more time resting and less time feeding during the summer months. The monkeys also spent more time moving during the summer months, shown by significant positive correlations with mean temperature and day length. Time spent feeding has a positive, and time spent moving a negative relationship with terrestriality. There were no significant correlations involving either fruit availability or time spent feeding from cheek pouches.

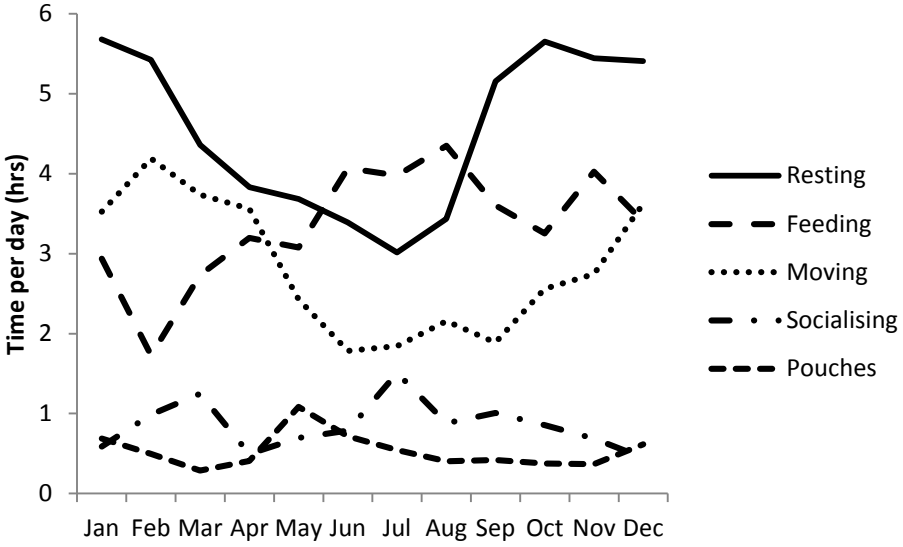

Figure 3.4 Mean monthly amount of time (hours) per day spent on different activities.

Table 3.6 Results from the correlation analysis for activity budget and environmental variables data. Variables used: mean monthly temperature (Mean Temp), monthly rainfall (Rain), day length, fruit availability (Fruit Avail), terrestriality (Terrestrial) and time spent resting, feeding, moving, socialising and eating from cheek pouches (Pouches). All significant correlations (p = <.05) are highlighted in bold. r = Pearson's correlation coefficient.

Variable	r / p	Mean Temp	Rain	Day Length	Fruit Avail	Terrestrial	Pouches	Socialising	Moving	Feeding
Resting	r	.879	.213	.933	-.444	-.520	-.248	-.354	.508	-.449
	p	**<.001**	.507	**<.001**	.148	.083	.437	.259	.092	.143
Feeding	r	-.651	-.111	-.407	-.400	.619	-.054	.016	-.789	
	p	**.022**	.732	.190	.197	**.032**	.868	.960	**.002**	
Moving	r	.804	.548	.648	.195	-.769	-.180	-.307		
	p	**.002**	.065	**.023**	.543	**.003**	.575	.331		
Socialising	r	-.329	-.634	-.351	.095	.276	-.290			
	p	.296	**.027**	.263	.769	.385	.361			
Pouches	r	-.310	-.185	-.308	.095	-.038				
	p	.326	.565	.331	.769	.907				

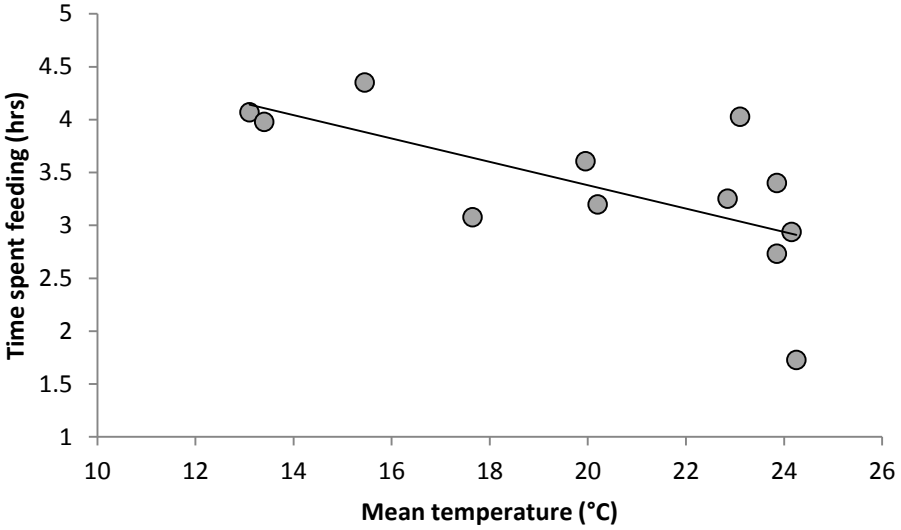

Figure 3.5 Relationship between time spent feeding and mean monthly temperature.

3.3.3 Diet

There are a number of previous samango studies which have reported diet composition data (Table 3.7). This study is one of only two to report fungi feeding in samango monkeys (Lawes et al. 1990). The data indicate a relatively low level of animal matter in the diet of the Lajuma samangos, along with the second highest proportion of leaf feeding. The monthly variation in diet composition (Figure 3.6) indicates a definite increase in leaf feeding during the winter months; however, there does not appear to be a strong pattern of fruit feeding seasonally. The food item which contributed the highest proportion of time feeding was the category "herb spp." a category including any small, non-tree species (Table 3.8). Herb species were always found at ground level and the samangos only consumed the leaves of the plants. Therefore, proportion of time spent feeding on herb species was included in the correlation analyses (Kolmogorov-Smirnoff p-value = .247) to investigate any potential effect on terrestriality or time spent feeding on leaves.

Table 3.7 Diet compositions from a number of different samango monkey studies. Figure for fruit % includes seeds (continues on next page).

Location	Study Length	Group Size	Fruit %	Leaves %	Flowers %	Other plant %	Animal %	Fungi %	Unknown %	Study
Budongo Forest, Uganda (logged forest)	13	-	55.8	21.8	4.6	9.3	8.6	0	0	Fairgrieve & Muhumuza 2003
Budongo Forest, Uganda (unlogged forest)	9	-	44.9	29.0	6.2	10.3	9.7	0	0	Fairgrieve & Muhumuza 2003
Kanyawara, Kibale Forest, Uganda	24	20.8	42.7	21.3	11.8	4.4	19.8	0	0	Rudran 1978
Kanyawara, Kibale Forest, Uganda	63	18.4	27.7	33.0	6.9	0	37.7	0	0.6	Butynski 1990
Ngogo, Kibale Forest Uganda	63	15	30.1	22.8	9.8	0	35.9	0	1.3	Butynski 1990
Kakamega Forest, Kenya	11	43	54.6	18.9	3.7	5.5	16.8	0	0.5	Cords 1986; 1987
Mgahinga Gorilla National Park, Uganda	6	-	26.3	51.6	0	4.6	16.3	0	1.2	Twinomigusha et al 2006
Kahuzi-Biega D.R.C	6	10	45.1	7.3	24.4	9.8	13.4	0	0	Schlichte 1978
Nyungwe Forest, Rwanda	10	27	47.4	6.2	6.2	0	24.9	0	6.2	Kaplin 2001
Diani Beach Forest, Kenya	6	-	57.1	7.1	14.3	21.4	0	0	0	Moreno-Black & Maples 1977

*Continued from previous page

Location	Study Length	Group Size	Fruit %	Leaves %	Flowers %	Other plant %	Animal %	Fungi %	Unknown %	Study
Zomba Plateau, Malawi	12	15	53.5	32.6	10.2	2.9	0.8	0	0	Beeson et al 1996
Entabeni Forest, S.A.	9	-	73.1	13	4.51	7.8	1.5	0	0	Breytenbach 1988
Ngoye Forest, S.A. (observational data)	12	16	91.1	3	2.1	0	0	0	3.8	Lawes et al. 1990
Ngoye Forest, S.A. (faecal data)	12	16	84.4	1.6	0.6	8.9	0.4	0.5	0	Lawes et al. 1990
Cape Vidal Forest, S.A.	13	32.5	51.7	25.8	13.4	0.9	5.8	0	2.3	Lawes 1991
Lajuma, S.A.	12	40	51.7	43.9	0.4	1.1	1.3	1.6	0	This study

Ch.3 Seasonal Variation in Basic Ecology

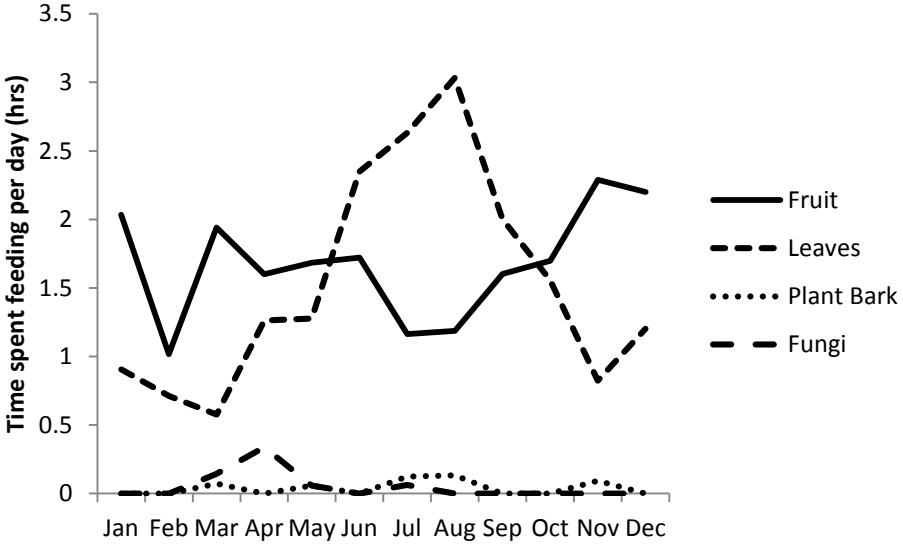

Figure 3.6 Mean monthly time (hours) per day feeding on different plant items.

Table 3.8 Top five most eaten plant species throughout the entire study period.

Species	% in diet
Herb spp.	21.3
Acacia ataxacantha	13.7
Ficus spp.	11.7
Rhus chirindensis	8.3
Rhoicissus tomentosa	7.3

Interestingly, time feeding on fruit had no significant correlations with any other variable (Table 3.9). Leaf eating was significantly positively correlated with feeding, whilst negatively correlated with resting and moving. Leaf eating also showed a significant negative correlation with mean temperature, indicating an increase in leaf consumption during the winter months (Figure 3.7). There was also a significant

positive relationship with terrestriality and significant negative relationships with both day journey length and journey speed. Time spent feeding on herb species was strongly significantly positively correlated with terrestriality (Figure 3.8, 3.9). There was also a significant negative correlation with mean temperature, indicating that herb species tend to be eaten more during the winter months.

Table 3.9 Results of the correlation analysis of diet components, environmental variables and activity budget data. Variables used: mean monthly temperature (Mean Temp), monthly rainfall (Rain), day length, terrestriality (Terrestrial), time spent feeding (Feeding) and resting (Resting), fruit availability (Fruit Avail), and time spent feeding on fruit, leaves, bark, fungi and herb species (Herb Spp.). All significant relationships (p = <.05) are highlighted in bold. r = Pearson's correlation coefficient.

Variable	r / p	Mean Temp	Rain	Day length	Terrestrial	Feeding	Resting	Fruit Avail	Herb Spp.	Fungi	Bark	Leaves
Fruit	r	.545	.471	.545	-.558	.128	.460	-.334	-.561	-.044	-.225	-.510
	p	.067	.122	.067	.059	.691	.133	.288	.058	.892	.482	.091
Leaves	r	-.686	-.860	-.686	.884	.737	-.639	-.148	.896	-.195	.401	
	p	**.014**	**<.001**	**.014**	**<.001**	**.006**	**.025**	.646	**<.001**	.544	.196	
Bark	r	-.355	-.428	-.355	.291	.489	-.530	-.188	.648	-.044		
	p	.258	.165	.258	.358	.107	.077	.558	**.023**	.891		
Fungi	r	-.284	-.002	-.284	-.188	-.156	-.362	.620	-.030			
	p	.372	.995	.372	.558	.627	.247	**.032**	.927			
Herb spp.	r	-.691	-.831	-.691	.863	.669	-.765	-.039				
	p	**.026**	**.001**	**.026**	**<.001**	**.017**	**.004**	.905				
Fruit avail	r	-.498	-.174	.084	-.083	-.400	-.444					
	p	.100	.588	.795	.798	.197	.148					

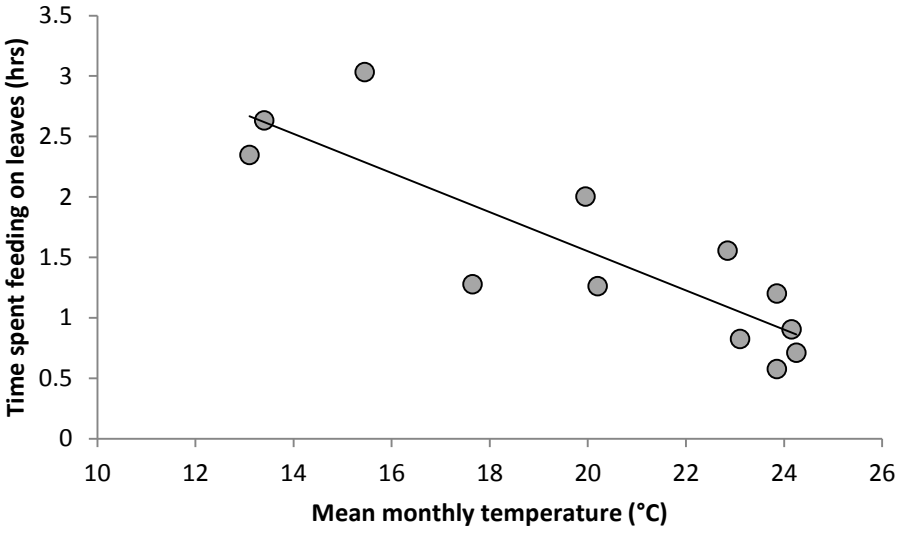

Figure 3.7 Relationship between leaf feeding and mean monthly temperature.

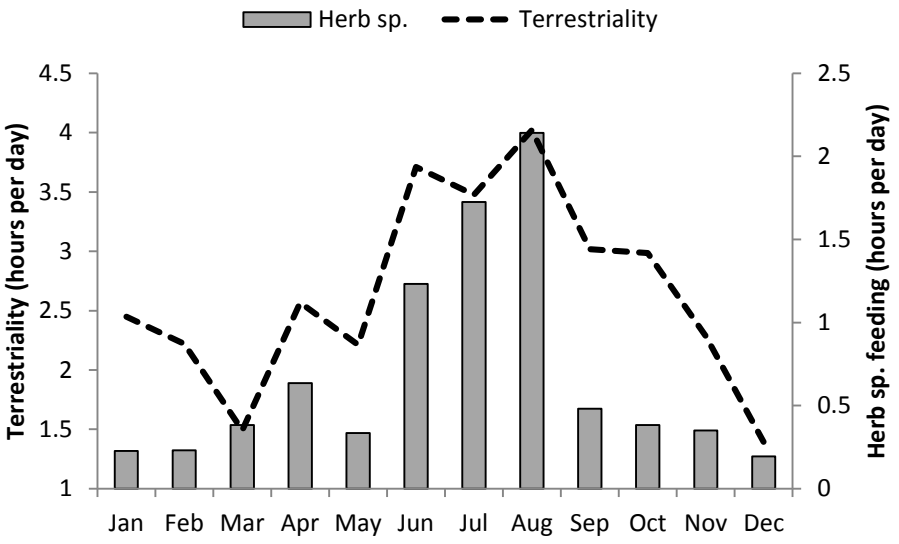

Figure 3.8 Seasonal trend of terrestriality and time spent feeding on herb species.

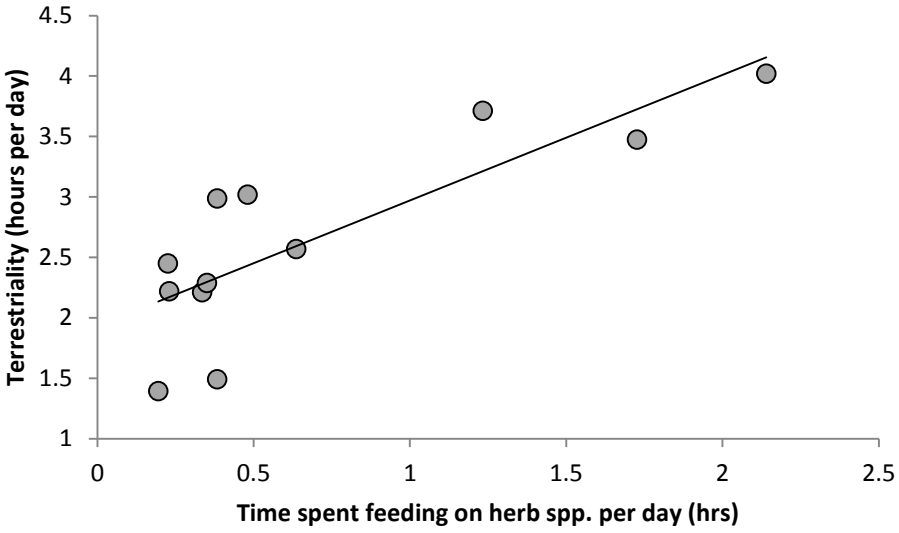

Figure 3.9 Relationship between time spent feeding on herb spp. and time spent terrestrial.

3.4 Discussion

The aim of this study was to investigate the effect a seasonal climate can have on the behavioural ecology of a group of samango monkeys which are located near the southern limit of their species' distribution. Being at the edge of their species range, it was expected that the samangos on site would be forced to adapt behaviourally to environmental conditions they may be less well adapted for evolutionarily (Sexton et al. 2009). The results of the study indicated that home range size did not significantly correlate with any climatic variables, although there was a significant negative correlation with fruit availability. Day journey length increased in the warm, wet summer months (October-April); however, this pattern is most likely due to increased day length than any climatic effect. Significant correlations with mean monthly temperature indicated that time spent feeding increased in the winter months, whilst time spent resting and moving decrease during this time. This increased time spent feeding appears to be feeding on leaves, as this also shared a significant negative correlation with mean monthly temperature.

3.4.1 Ranging

A number of previous primate studies have observed a discernible decrease in ranging during lower fruit availability months (Rudran 1978, Stanford 1991, Doran 1997, Hanya 2004, Li et al. 2010). The most common reason attributed to this pattern was the attempt to reduce energy expenditure when fruit availability is low. However, the results from this study indicate that samangos increase home range size at times of lower fruit availability. Blue-eyed black lemurs (*Eulemur flavifrons*) have been observed to increase their home range size during a period of low fruit availability (Volampeno et al. 2011) as have black crested mangabeys (*Cercocebus albigena*) (Waser 1977). Waser (1977) suggested the reason for this pattern was the mangabeys were attempting to access larger, more widely scattered fruiting trees, including fig species. For the samangos, during the lowest fruit availability months, the most eaten fruiting trees were also large, widely distributed species (*R. chirindensis* and fig spp.). Therefore, the samangos may be increasing home range size in order to access more individuals of these species. However, the lemurs and mangabeys also increased day journey length significantly during periods of low fruit availability, a pattern not observed in the samangos. This suggests that the samangos may have used a localised area each day, but moved to new areas of the range on subsequent days; in doing so they maximise range area without increasing daily journey lengths. Journey speed was observed to decrease during winter months, most likely caused by the reduction in overall time spent moving during these months. The monkeys feed on herb species more during the winter months and as herb species tend to be at ground level this is the likely reason for increased time spent terrestrial during this period. This is also the likely reason for the positive relationship observed between time spent feeding on leaves and terrestriality, as all herb feeding was counted as leaf material.

3.4.2 Activity budgets

No previous samango monkey study has reported seasonal variation in activity budget data. This study has therefore allowed an interesting insight into how

environmental factors may affect how samango monkeys apportion their time to different activities. A number of previous primate studies have observed an effect of food availability on activity budget (Garber 1993, Doran 1997, Hill 1997, Gursky 2000, Guo et al. 2007, Chaves et al. 2011), but the results of this study showed no evidence of such a pattern. However, an interesting pattern which was observed was an increase in time spent feeding on leaves during winter months. In many instances this relationship would likely be explained by a shift from a mostly frugivorous to a mostly folivorous diet (Fairgrieve 1995, Beeson et al. 1996). Leaves, due to their fibrous nature, are often more difficult to consume and digest and therefore more time might have to be spent processing the material (Milton 1981). However, fruit feeding does not decrease in the winter months in the samangos. Therefore, the increase in feeding time likely indicates the samangos simply consume more during the winter months. Living at such southerly latitude and at an altitude of approximately 1200m, the samangos at Lajuma have to survive relatively cold winters, when compared to other populations of *C. mitis* (Table 3.10). As a result, the reason for an increase in feeding during winter months may be due to the elevated energetic requirements of maintaining their body temperatures in the cold period. Geladas exhibit a similar pattern of increasing feeding times at higher altitudes for thermoregulatory reasons (Iwamoto & Dunbar 1983). Another possibility is variation in nutritional composition of different fruit species (Johnson et al. 1985), but unfortunately these data were not available for this study.

Whilst the most likely reason for the increase in time spent resting during summer months is the increase in day length, the effect of high temperature must also be considered a possible reason for this increase. Temperatures in shade sometimes exceeded 40°C in the summer and such high temperatures may have contributed to the increased resting time observed. Similar patterns of increased time spent resting due to high temperatures have previously been documented in baboons (Stelzner & Hausfater 1986, Pochron 2000, Hill 2006) and white-faced capuchins (Campos & Fedigan 2009). Within these examples individuals exposed to high temperatures

would spend time resting in shaded areas and the samangos at Lajuma may therefore be exhibiting a similar behaviour.

Table 3.10 Mean lowest temperatures of the coldest months at various samango monkey study sites. Data extracted from Hijmans et al (2005).

Location	Lowest Temp (°C)	Study
Diani Beach Forest, Kenya	20.4	Moreno-Black & Maples 1977
Kakamega Forest, Kenya	15.3	Cords 1986
Kanyawara, Kibale Forest, Uganda	12.7	Rudran 1978
Cape Vidal Forest, S.A.	11.6	Lawes 1991
Zomba Plateau, Malawi	9.2	Beeson et al 1996
Mgahinga Gorilla National Park, D.R.C.	6.4	Twinomigusha et al 2006
Lajuma, South Africa	3.8	This study

3.4.3 Diet composition

A large number of primate studies have reported non-fruit items being used to supplement lower fruit feeding during times of low fruit availability (Hladik 1975, Milton 1980, Stanford 1991, Garber 1993, Galetti & Pedroni 1994, Hill 1997, Peres 2000). However, the results of this study show no significant correlation between time spent feeding on any of the diet components and fruit availability. As mentioned previously, during the months of lower fruit availability the species which contribute most to the fruit diet of the monkeys tend to be large, isolated trees. Therefore, whilst overall fruit biomass might be lower during some months, plenty of fruit is still available to the monkeys as long as they are able to locate individuals of these species. This would explain why fruit feeding does not decrease from the period of October to January when overall fruit availability is lower.

3.4.4. Conclusions

The samango monkeys on site represent an isolated population close to the southerly limit of what is a wide ranging primate species (Kingdon et al. 2008c). The location, in terms of latitude and altitude, means the samangos experience a highly seasonal climate with cold, dry winters. To survive in these conditions the samangos must adapt their behaviour correspondingly, such as by increasing time spent feeding during the colder months. This study has also shown that such isolated populations might not conform to predictions based on populations from other locations. For example Rudran (1978), Beeson et al. (1996) and Lawes (1991) both observed a decrease in fruit feeding by samangos during their respective dry seasons; however, this study showed no significant effects of climate on fruit feeding.

The majority of samango monkey long term behavioural studies have been conducted in equatorial countries such as Uganda (Rudran 1978, Butynski 1990, Fairgrieve & Muhumuza 2003, Twinomugisha et al. 2006), Kenya (Moreno-Black & Maples 1977, Cords 1987) and the Democratic Republic of Congo (Schlichte 1978). However, it is important to compare data from locations throughout a species' distribution, in order to gain a strong indication about how the basic ecology of different populations might differ or be similar. This will be the subject of the next data chapter, which investigates the biogeographical variation in *C. mitis* behavioural ecology.

Chapter 4

Biogeographical Determinants of Behavioural Ecology

4.1 Introduction

4.1.1 Geographical diet variation

An important question in animal ecology is how diet varies temporally within a single population, either in terms of seasonal variation (Hill 1997, Whitaker et al. 1999, Hirsch 2009) or annual variation (Hedd et al. 2002, Lorentsen et al. 2004). Such studies allow for the comparison of how populations adapt behaviourally to the varying environmental conditions they experience. However, the study of diet variation across more than one population allows for a more in depth comparison of the biogeographical effects on a key aspect of behavioural ecology (Tixier & Duncan 1996, Gebert & Verheyden-Tixier 2001, Chapman et al. 2002, Hill & Dunbar 2002). Understanding these biogeographical effects is important in understanding species distributions, diversity and evolution (Mittelbach et al. 2007).

Previous studies examining inter-population variation in mammalian diets have tended to focus on carnivores, for example, Lozano et al. (2006) showed that European wildcat (*Felis silvestris silvestris*) diet becomes more diverse in warmer climates; whilst Vulla et al. (2009) observed that the proportion of meat in the diet of brown bears (*Ursus arctos*) increases in colder climates. Other carnivore study species have included Eurasian otters (*Lutra lutra*) (Clavero et al. 2003), genets (*Genetta genetta*) (Virgos et al. 1999), European badgers (*Meles meles*) (Goszczynski et al. 2000) and other mustelidae species (Zhou et al. 2011). Only a limited number of

non-carnivore studies have focused on geographical variation in diet. For example, Swedish bank voles (*Myodes glareolus*) in northerly areas, where seeds become less abundant, switch their diets to include more frugivorous items such as berries (Hansson et al. 2000). Similarly, wild boars are able to survive in climatically difficult areas in northerly latitudes due to their omnivorous nature (Melis et al. 2006). These studies indicate that if a species has a large enough distribution, diet variation throughout that distribution is likely, if not inevitable; which presents an interesting study topic into the environmental causes of this variation and the potential evolutionary consequences.

In primates, different aspects of climate have been shown to partially explain variation in a number of aspects of behavioural ecology. For example, rainfall is an important determinant of spider monkey (*Ateles* spp.) party size and coupled with temperature variation also partially explains variation in activity budgets (Korstjens et al. 2006). Mean annual temperature has also been shown to partially explain baboon (*Papio* spp.) inter-birth intervals (Hill et al. 2000). In one of the only studies to investigate macro-spatial variation in the diet of a primate species, Hill & Dunbar (2002) used data on 15 populations of baboons to assess the relationship between dietary composition and environmental variables. They found that the proportion of time spent feeding on fruit by baboons increases with increasing mean temperature, decreasing altitude and with increasing P.P.I. (Primary Productivity Index), a measurement indicating the number of productive months in a year. Their results also showed that time spent eating leaves and subterranean foods had a negative relationship with temperature, indicating their status as "fall-back" foods, eaten when fruit is limiting. In a study of gorillas (*Gorilla* spp.), Lehmann et al. (2008) observed that in areas of low fruit availability gorillas spend more time resting, due to the increased digestive effort associated with elevated leaf consumption.

Another important and potentially geographically variable dietary component is diet diversity. Areas which have high primary productivity are also likely to have high plant species richness (Currie 1991, Kay et al. 1997, Hawkins et al. 2003). This should

be evident in the diets of the animals' resident in these areas. Whilst this seems a logical inference little work has been conducted researching this possible link, suggesting a potential future avenue for research.

The studies mentioned indicate that geographically variable climatic conditions can have significant effects on a genus' or species' diet. Such studies allow for researchers to investigate how species have to adapt behaviourally to survive different environmental conditions and the affect this has on species distributions and eventually evolution (Altmann 1974b). This study is the one of the first to attempt such an investigation focussing on a monkey species, and the first focussing on samango monkeys as a focal species.

4.1.2 Samango monkeys

The distribution of samango monkeys extends from central Ethiopia in the north to the Eastern Cape, South Africa, in the south, a range of approximately 5000km, and west-east from western Angola to Somalia approximately 3200km (Figure 4.1). Most forest guenons tend to have diets strongly dominated by fruit (Gautier-Hion 1988, Beeson et al. 1996, Chapman et al. 2002), but samango monkeys tend to have a broader diet when compared with other arboreal Cercopithecine species (Chapman et al. 2002). Samangos supplement their diet from a variety of different sources such as leaves (Fairgrieve 1995, Beeson et al. 1996); insects (Butynski 1990, Kaplin 2001) and flowers (Schlichte 1978). The leaf eating data are reflected in the gut morphology of samangos, which have longer caecums, larger numbers of cellulases and more cellulose digesting bacteria than other Cercopithecines (Bruorton et al. 1991). This indicates that samangos have evolved to digest a diet with a higher proportion of foliar material. The different climates throughout the large distribution of *C. mitis* may account for the large variation in the diets in various populations (see Table 4.1). By investigating how geographically variable climatic conditions affect samango diet composition it may be possible to draw conclusions on why samango monkeys have

been able to range further south than any other arboreal guenon species (Wolfheim 1982).

C. m. erythrarchus are one of the most southerly sub-species of samango monkey, ranging throughout Mozambique, Zimbabwe and northern South Africa (Figure 2.4). As a consequence they experience a highly seasonal climate. A previous chapter has shown that *C. m. erythrarchus* increase their leaf consumption during colder months to subsidise their normally highly frugivorous diet (Section 3.3.3). Sub-species living closer to the equator, such as *C. m. stuhlmanni*, do not experience such cold temperatures and so may not need to subsidise their diet with as many non-fruit items. This relationship may not, however, be as simple as the amount of fruit available to the monkeys. For example, fruit contains very little protein (Milton 1981, Rogers et al. 1990, Oftedal 1991) and so samango monkeys, even in tropical regions, will likely have to supplement their diets with non-fruit items that have higher protein content, such as animal matter.

At the southern limit of the samango species' range, climatic conditions become highly seasonal; characterised by cold, dry winters (Willems 2007). The samangos residing in these areas may be forced to move from the highly frugivorous diets associated with most arboreal guenon species (Chapman et al. 2002). As samangos are better evolved for leaf consumption than most other Cercopithecines (Bruorton et al. 1991), the populations living in these southern areas may supplement their diet with a higher proportion of leaves than more tropical populations. Diet diversity may also be an observable factor in samango diets, and as there is a common trend of increasing species richness towards the tropics (Hawkins et al. 2003), it would be expected that samango populations in more tropical areas should also have a more diverse diet in terms of number of plant species consumed.

4.1.3 Objectives

The overall aim of this study is to investigate the environmental factors which cause diet composition variation between different populations of a widely distributed arboreal primate species. This study will allow the comparison of populations resident in a variety of habitats which vary substantially in their environmental conditions. Previous primate studies investigating baboons (Hill & Dunbar 2002) and gorillas (Lehmann et al. 2008) have shown that geographically varying climatic conditions can be an important driver of diet composition variation, but to date no study had examined how these relationships might extend to arboreal primate species. In fact this study is the first of its kind to attempt such a comparison in populations of a single primate species. This study therefore addresses this gap in the literature and will test the following predictions:

1) Proportion of fruit in the diet of samangos will increase in more tropical environments.
2) In non-tropical environments, where fruit consumption is lower, leaves will supplement the diet.
3) In more tropical areas dietary diversity will increase.

4.2 Methods

Data on diet composition, climate and some behavioural data were available for 12 populations of *Cercopithecus mitis* (Tables 3.3, 4.1, 4.2, Figure 4.1). Diet components were separated into fruits (including seeds), leaves, flowers, other plant (e.g. bark), animal matter (usually invertebrates, e.g. caterpillars, ants), fungi and unknown. The statistics reported in Table 4.1 correspond to the proportion of the diet these components comprise in each population, through either direct observation of feeding, faecal analysis or, as in one study, investigation of the stomach contents of deceased monkeys. Finally, where the data were available, the percentage

contribution of the top 10 most eaten species to the diet was calculated to represent dietary diversity.

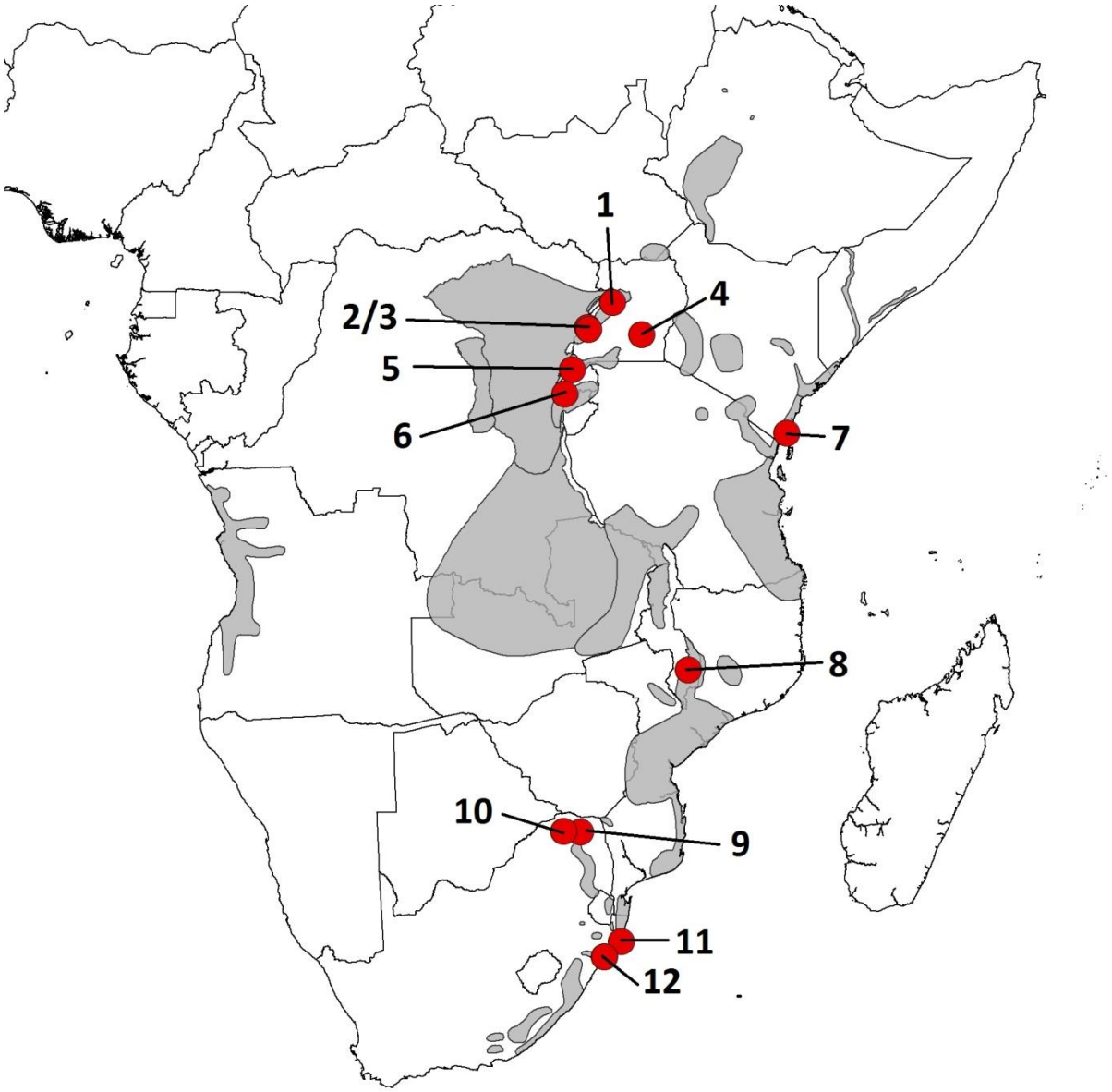

Figure 4.1 Map showing locations of the *C. mitis* sites used in this study (red circles) and the known distibution of the species in grey (Kingdon et al. 2008c). See Table 4.1 for details of numbered populations.

4.2.1 Climatic data

Climatic data for Africa were extracted from a dataset at a resolution of 30s of a degree (equating to 0.86km^2 at the equator) based on detailed climatic data from 1950-2000 (Hijmans et al. 2005). The selected climatic variables were mean annual temperature, diurnal temperature range (mean of monthly (max temp – min temp), temperature seasonality (standard deviation of mean temp), maximum temperature of warmest month, minimum temperature of coldest month, annual temperature range (max temp warmest month – min temp coldest month), annual precipitation, precipitation seasonality (coefficient of variation) and altitude. Along with these bioclimatic variables the Primary Productivity Index (P.P.I.) was calculated (Le Houerou 1984). P.P.I. is a good indicator of the length of a growing season and is defined as the number of months in which total precipitation (in mm) exceeded twice the mean annual temperature (in °C) for that site. Finally, day length variation (length of longest day – length of shortest day) was calculated using data from the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/Dur_OneYear.php). These variables were chosen after assessment of indices used by three previous cross-populational primate studies (Williamson & Dunbar 1999, Hill & Dunbar 2002, Willems & Hill 2009a).

There were very strong positive correlations between some climate variables (Table 4.3). As a result the original 11 climatic variables were reduced to six principal variables – altitude, mean annual temperature, temperature seasonality, mean annual precipitation, diurnal temperature range and P.P.I. - to minimise the confounding effects of having strongly correlated climatic variables present in further analyses. Previous studies have highlighted potential problems with multiple tests (Hochberg 1988, Bland & Altman 1995a). However, all the correlation analyses used in this study were not corrected for multiple testing due to the potential problems associated with the correction methods, such as increased Type II errors (Perneger 1998, Moran 2003, Nakagawa 2004).

Table 4.1 Diet composition data from all available *C. mitis* studies with a minimum study period of 6 months. Listed are location of sites, type of study and proportion of different food types in diet. In data type column, Obs = Observations, Fae = Faecal analysis and Sto = Stomach content analysis of deceased specimens. Some figures are averages of more than one group. Pop = Population number (Figure 4.1).

Location	Pop	Latitude	Longitude	Data type	Study Period (months)	% of diet from top 10 species	Number of plant species	Fruit % (inc seeds)	Leaves %	Flowers %	Other plant %	Animal %	Fungi %	Unknown %	Study
Budongo Forest, Uganda	1	1°35'-1°55'N	31°18'-31°42'E	Obs	13	69.6	40	44.9	29.0	6.2	10.3	9.7	0	0	Fairgrieve and Muhumuza 2003 (unlogged forest)
Kanyawara, Kibale Forest, Uganda	2	0°34'N	30°21'E	Obs	24	60.9	59	42.7	21.3	11.8	4.4	19.8	0	0	Rudran 1978
Kanyawara, Kibale Forest, Uganda	2	0°34'N	30°21'E	Obs	63	-	40	27.7	33.0	6.9	0	37.7	0	0.6	Butynski 1990
Ngogo, Kibale Forest Uganda	3	0°13'-0°41'N	30°19'-30°32'E	Obs	63	-	52	30.1	22.8	9.8	0	35.9	0	1.3	Butynski 1990
Kakamega Forest, Kenya	4	0°14'N	32°52'E	Obs	11	-	104	54.6	18.9	3.7	5.5	16.8	0	0.5	Cords 1986; 1987
Mgahinga Gorilla National Park, Uganda	5	1°23'17''S	29°38'31''E	Fae	6	-	33	26.3	51.6	0	4.6	16.3	0	1.2	Twinomigusha et al 2006
Nyungwe Forest, Rwanda	6	2°17'-2°50'S	29°07'-29°26'E	Obs	8	83.9	59	47.4	6.2	6.2	0	24.9	0	6.2	Kaplin 2001
Diani Beach Forest, Kenya	7	4°17'S	39°35'E	Obs/ Fae	6	-	27	57.1	7.1	14.3	21.4	0	0	0	Moreno-Black & Maples 1977
Zomba Plateau, Malawi	8	15°20'S	35°19'E	Obs	12	-	33	53.5	32.6	10.2	2.9	0.8	0	0	Beeson et al 1996
Entabeni Forest, S.A.	9	23°02'S	30°17'E	Sto	9	-	-	73.1	13	4.51	7.8	1.5	0	0	Breytenbach 1988
Lajuma, South Africa	10	23º02'23''S	29º26'05''E	Obs	12	70.0	35	51.7	43.9	0.4	1.1	1.3	1.6	0	This study (adult scan data)
Cape Vidal Forest, S.A.	11	28°05'35''S	32°33'40''E	Obs	13	77.9	57	51.7	25.8	13.4	0.9	5.8	0	2.3	Lawes 1991
Ngoye Forest, S.A.	12	28°50'S	31°42'E	Obs	12	84.5	30	91.1	3.0	2.1	0	0	0	3.8	Lawes et al 1990 (observation)
Ngoye Forest, S.A.	12	28°50'S	31°42'E	Fae	12	-	30	84.4	1.6	0.6	8.9	0.4	0.5	0	Lawes et al 1990 (faecal)

Table 4.2 *C. mitis* study sites used in the analyses; includes data on day length variation (http://aa.usno.navy.mil/data/docs/Dur_OneYear.php), altitude and climate variables at each site (Hijmans et al. 2005).

Location	Day length variation (mins)	Altitude (m)	Mean annual temp (°C)	Diurnal temp range (°C)	Temp seasonality (°C)	Highest temp of warmest month (°C)	Lowest temp of coldest month (°C)	Annual temperature range (°C)	Mean annual precipitation (mm)	Precipitation seasonality (mm)	P.P.I.
Budongo Forest, Uganda	12	1079	23.0	11.8	7.92	31.1	16.5	14.6	1330	43	9
Kanyawara, Kibale Forest, Uganda (Rudran)	3	1503	19.5	12.0	4.17	26.9	12.7	14.2	1446	44	12
Kanyawara, Kibale Forest, Uganda (Butynski)	3	1503	19.5	12.0	4.17	26.9	12.7	14.2	1446	44	12
Ngogo, Kibale Forest Uganda	3	1450	20.7	12.2	3.18	27.6	13.9	13.7	1267	38	12
Kakamega Forest, Kenya	2	1144	21.5	10.8	5.40	28.3	15.3	13.0	1455	33	12
Mgahinga Gorilla National Park	9	2989	11.5	9.8	2.49	17.0	6.4	10.6	1823	42	12
Nyungwe Forest, Rwanda	18	2298	15.5	9.6	3.51	21.5	9.9	11.6	1663	51	11
Diani Beach Forest, Kenya	30	14	26.6	8.2	1.44	33.1	20.4	12.7	1277	79	10
Zomba Plateau, Malawi	131	1737	17.2	9.4	1.88	25.0	9.2	15.8	1416	96	6
Entabeni Forest, S.A.	170	740	20.6	11.6	2.70	29.0	9.4	19.6	899	84	6
Lajuma, South Africa	170	1372	17.0	12.9	3.35	26.1	3.8	22.3	799	83	7
Cape Vidal Forest, S.A.	215	72	21.3	9.3	2.72	29.4	11.6	17.8	1063	37	12
Ngoye Forest, S.A.	221	417	19.6	9.9	2.39	27.3	10.5	16.8	1140	44	10

Table 4.3 Results of correlation analysis between all climatic variables, altitude and day length. Correlations based on data extracted for each study population. Where used Temp = Temperature. Significant correlations (p=<.05) are presented in bold. r = Pearson's correlation coefficient, N = 12.

Variable	r / p	P.P.I.	Precipitation seasonality	Mean annual precipitation	Temp range	Lowest temp of coldest month	Highest temp of warmest month	Temp seasonality	Diurnal temp range	Mean annual temp	Day length
Altitude	r	.135	-.084	.689	-.438	-.519	-.896	-.552	.162	-.861	-.490
	p	.646	.795	**.013**	.155	.084	**<.001**	.063	.616	**<.001**	.106
Day length variation	r	-.475	.336	-.735	.793	-.441	.168	.924	-.073	.013	
	p	.086	.286	**.006**	**.002**	.151	.601	**<.001**	.821	.967	
Mean annual temperature	r	-.026	.038	-.421	.118	.835	.973	.155	-.096		
	p	.929	.907	.173	.714	**.001**	**<.001**	.629	.766		
Diurnal temperature range	r	-.097	-.047	-.360	.461	-.303	.049	.062			
	p	.742	.884	.250	.131	.338	.880	.848			
Temperature seasonality	r	-.636	.530	-.885	.908	-.380	.324				
	p	**.014**	.077	**<.001**	**<.001**	.223	.304				
Highest temp warmest month	r	-.165	.122	-.594	.332	.699					
	p	.572	.706	**.042**	.292	**.011**					
Lowest temp coldest month	r	.327	-.233	.144	-.443						
	p	.254	.467	.655	.150						
Temperature range	r	-.632	.460	-.934							
	p	**.015**	.133	**<.001**							
Mean annual precipitation	r	.551	-.413								
	p	**.041**	.182								
Precipitation seasonality	r	-.860									
	p	**<.001**									

4.2.2 Statistical analysis

Correlation analysis

A parametric correlation analysis was conducted to investigate bivariate relationships between the six climatic variables, home range size, group size, diet composition and the contribution of the top ten most eaten plant species to the overall plant diet. Kolmogorov-Smirnoff tests showed that all diet components but fungi were normally distributed (Table 4.4). Only two studies reported fungi being consumed and thus fungi was not included as a response variable in the analysis. Day journey length and activity budget data were not included in this analysis due to insufficient sample sizes (Table 3.3).

Only studies with duration of at least 6 months were included in the analyses. For Fairgrieve & Muhumuza (2003) only unlogged forest data were used, as this is more comparable to other study sites. Lawes et al. (1990) used two different methods, so each data set was given a weighting of 0.5. Finally, two studies were conducted 12 years apart at Kanyawara, Kibale Forest, Uganda and so each were given weighting of 0.5 (Rudran 1978, Butynski 1990).

Due to the potential Type I errors caused by multiple testing, all statistically significant correlations will only be discussed based on the hypotheses made and the biological merit of the significantly correlated relationships. All correlations will also only be accepted as significant if the effect size is substantial (i.e. minimum r = .5) (Nakagawa 2004).

Table 4.4 Results of Kolmogorov-Smirnoff test for normality for diet variables.

Diet component	Fruit	Leaves	Flowers	Other Plant	Animal	Fungi
p	.536	.870	.914	.606	.603	**.001**

4.3 Results

4.3.1 Activity budget

Due to a lack of available data (n=5) no correlations were calculated involving activity budget data (Table 3.3). However, the large range within variables indicates the potential for significant patterns, should more data become available. For example, proportion of time feeding ranges from 28.1% of time in Lajuma, South Africa (this study), to 49.1% of time in Kakamega Forest, Kenya (Cords 1986).

4.3.2 Linear correlation analysis

Proportion of fruit in the diet of samangos shares significant negative relationships with proportion of animal matter and leaves (Table 4.5), indicating that in populations where fruit comprises less of the overall diet, the diet is likely to comprise increased levels of animal matter and/or leaf material. Amount of leaf material in the diet shares no other significant relationships with any of the other variables. Proportion of fruit in the diet has a significant positive relationship with temperature seasonality (Figure 4.2). This is the opposite relationship shared with proportion of animal matter which has a significant negative relationship with temperature seasonality (Figure 4.3). Amount of animal matter also has a significant positive relationship with P.P.I. (Figure 4.4). Proportion of flowers in the diet shares no significant relationships with any of the variables investigated, whilst the category "other plant" shares a significant positive relationship with mean annual temperature. There were no significant correlations involving home range or group size.

The variable used to represent diet diversity (% of diet comprised by the top ten most eaten species) shared no significant relationships with any other variables. There is, however, a strong negative trend with diurnal temperature range (Figure 4.5). The possible causal links between diurnal temperature range and dietary diversity are not at first apparent, therefore, to investigate this further a backwards regression

analysis was conducted to see which climatic factors mostly likely contribute to diurnal temperature range. The results of this analysis can be seen in Table 4.6 and indicate that areas of high diurnal temperature range are also likely to have low mean annual precipitation, low temperature seasonality and high altitude.

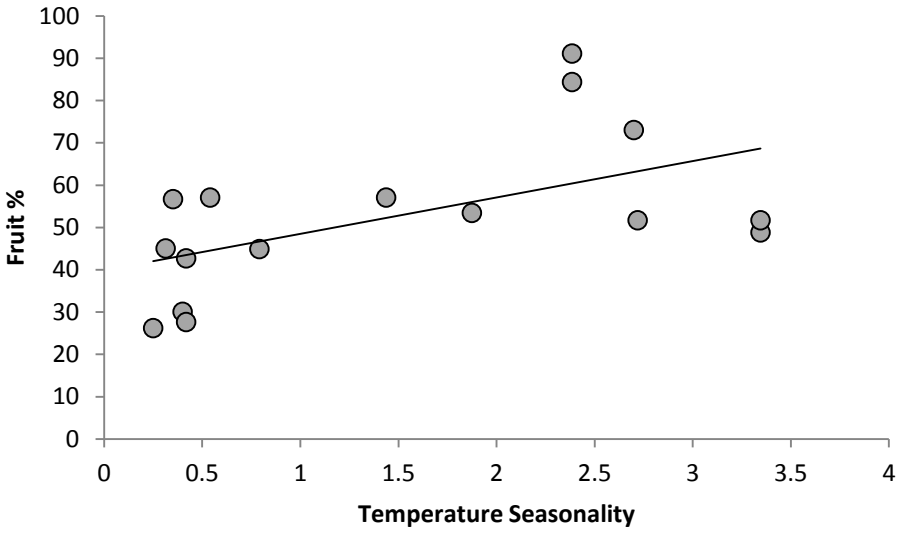

Figure 4.2 Relationship between temperature seasonality and % fruit in the diet of samangos with linear line of best fit.

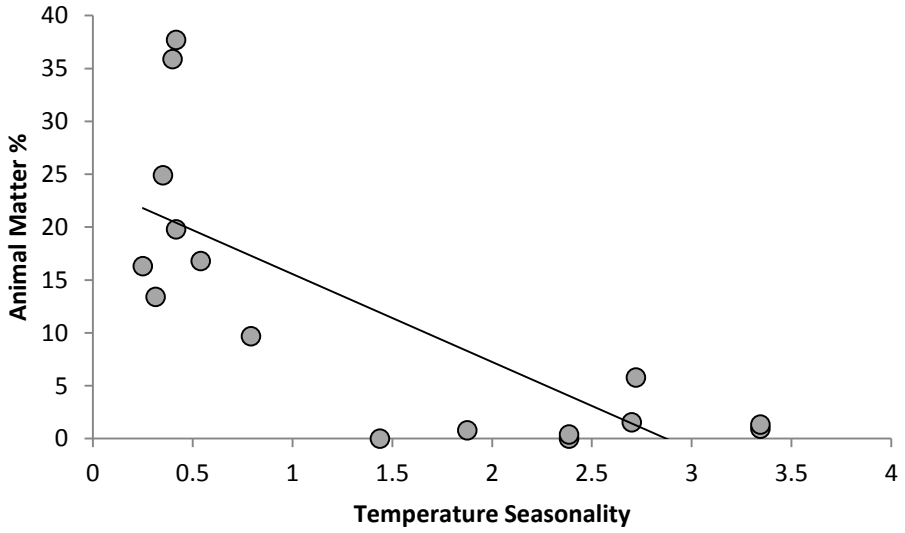

Figure 4.3 Relationship between temperature seasonality and % animal matter in the diet of samangos with linear line of best fit.

Table 4.5 Correlations between selected climatic variables, diet composition, home range and group size. For % of diet from top ten species n=6, home range and group correlations size n=8, for all other correlations n=12. Variables within table are altitude, mean annual temperature (Mean Annual Temp), diurnal temperature range (Diurnal Temp Range), temperature seasonality (Temp Seas), mean annual precipitation (Mean Annual Prec), Primary Productivity Index (P.P.I.), home range, group size, proportion of diet made up by the top ten most eaten species (% Diet From Top 10) and proportion of diet contributed by the categories fruit, leaves, animal matter, flowers and other plant. Significant correlations (p=<.05) presented in bold.

Variable	r / p	Altitude	Mean Annual Temp	Diurnal Temp Range	Temp Seas	Mean Annual Prec	P.P.I.	Group Size	Home Range	% Diet From Top 10	Other Plant %	Flowers %	Animal %	Leaves %
Fruit %	r	-.599	.303	-.226	.583	-.503	-.403	-.063	-.425	.729	.184	-.135	-.649	-.692
	p	.059	.339	.480	**.047**	.096	.153	.862	.254	.100	.567	.677	**.022**	**.013**
Leaves %	r	.540	-.537	.342	-.024	.135	.028	.299	-.348	-.640	-.293	-.299	.085	
	p	.070	.072	.276	.941	.676	.926	.401	.359	.171	.355	.345	.792	
Animal %	r	.490	-.243	.297	-.765	.550	.646	-.122	.607	-.142	-.456	.042		
	p	.106	.447	.349	**.004**	.064	**.013**	.737	.083	.788	.209	.897		
Flowers %	r	-.451	.576	-.411	-.069	-.006	.173	-.205	.096	-.277	.293			
	p	.141	.050	.185	.832	.985	.554	.569	.806	.595	.355			
Other Plant %	r	-.439	.615	-.372	.022	-.075	.202	-.151	-.421	-.599				
	p	.154	**.033**	.234	.945	.816	.490	.678	.260	.209				
% Diet From Top 10	r	-.153	-.287	-.807	.200	.080	.085	-.132	.246					
	p	.772	.581	.052	.704	.881	.874	.832	.690					
Home Range	r	.340	-.208	.219	-.370	.170	.334	-.353						
	p	.370	.591	.572	.327	.661	.380	.391						
Group Size	r	.006	.061	.168	.157	-.220	.047							
	p	.986	.867	.642	.664	.541	.897							

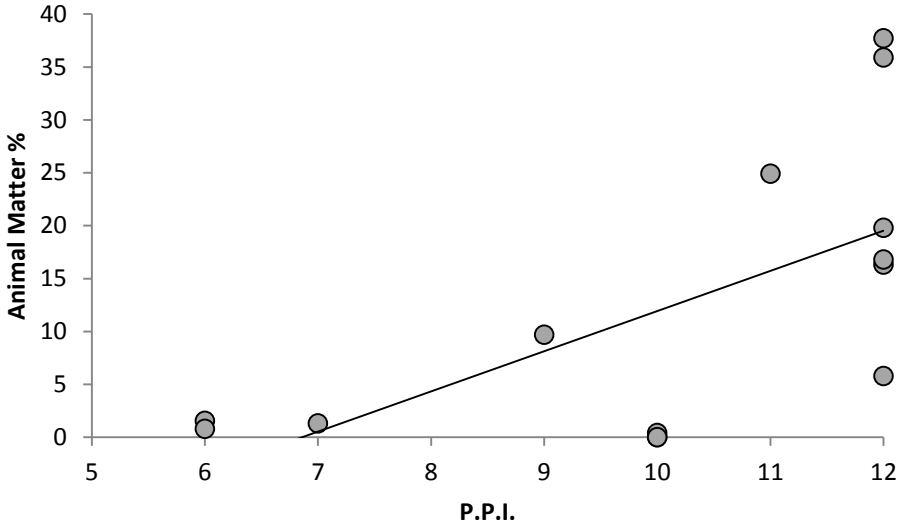

Figure 4.4 Relationship between Primary Productivity Index (P.P.I.) and % animal matter in the diet of samangos with linear line of best fit.

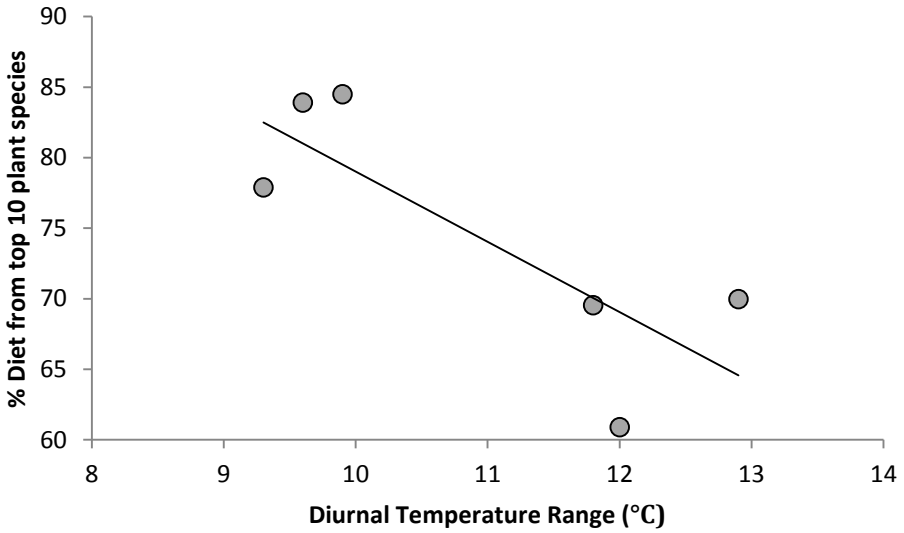

Figure 4.5 Relationship between contribution of top ten most eaten plant species to the total plant diet and diurnal temperature range in six different *C. mitis* populations.

Table 4.6 Results of backwards regression with diurnal temperature variation as the response variable. R = .938, Adjusted R^2 = .835.

Predictor	B	β	t	p
Mean annual precipitation	-.011	-2.272	-7.395	**<.001**
Temperature Seasonality	-1.819	-1.432	-5.359	**.001**
Altitude	.002	.936	5.457	**.001**

4.3.3 Equations

Regression equations were derived to predict how proportion of animal matter and fruit should vary in the diet of samangos throughout the entire species' distribution.

Animal % = (−8.740 × Temperature seasonality) +24.372

R = .765, Adj R^2 = .543, F = 14.088, t = -3.753

Fruit % = (9.035 × Temperature seasonality) +39.136

R = .583, Adj R^2 = .274, F = 5.144, t = -2.268

These equations were used to create GIS maps displaying the predicted distributions of these diet components throughout the species' range (Figure 4.6). The maps indicate that temperature seasonality becomes more pronounced in southerly latitudes, which in turn has an effect on the proportion of fruit and animal matter in samango monkey diet. The equations suggest that fruit in the diet generally should not exceed approximately 80% or drop below approximately 40%. The equations also indicate that below latitude of approximately 11°S, in countries such as Mozambique and South Africa, there should be very little animal matter in the diet.

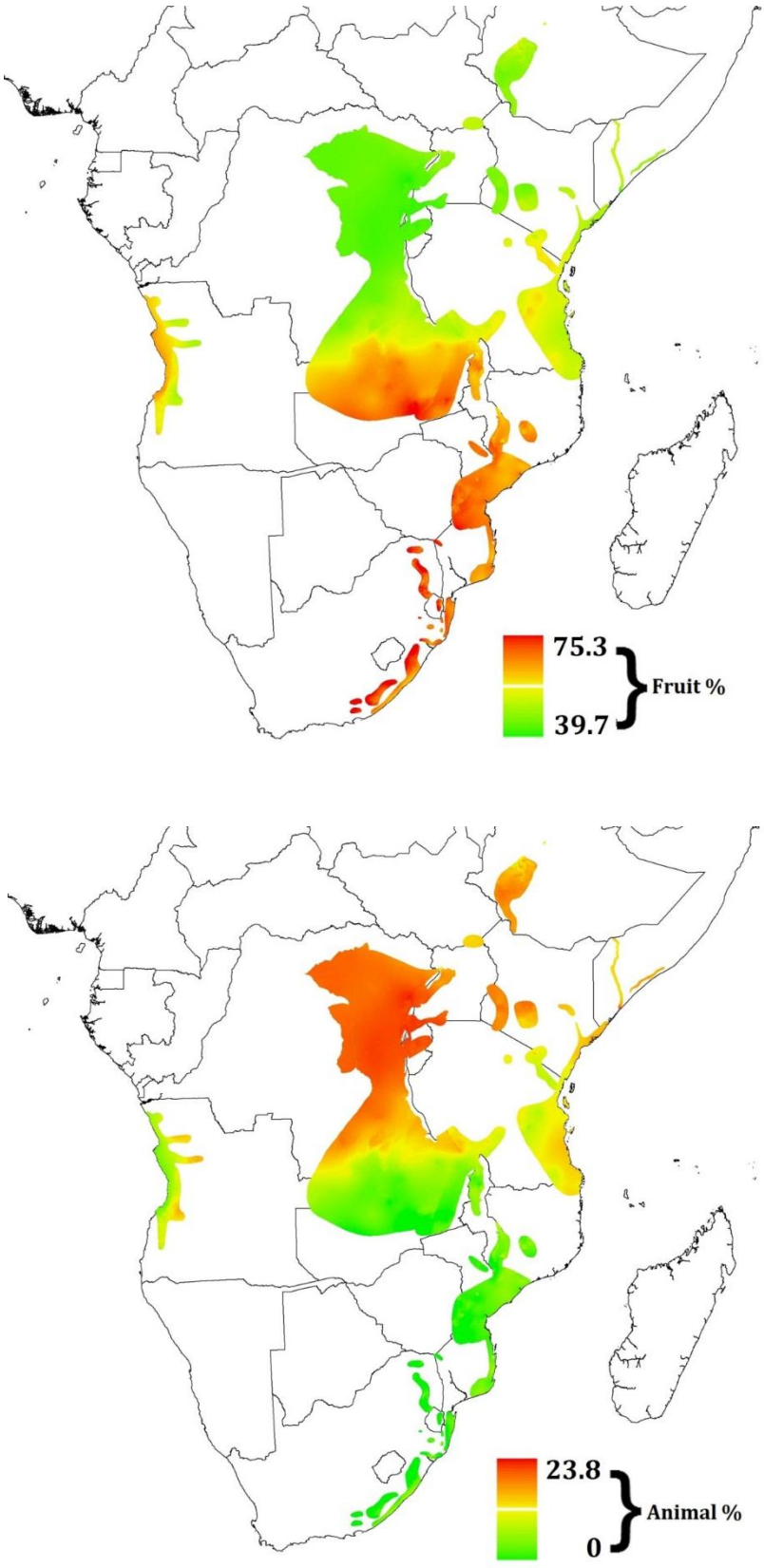

Figure 4.6 Predicted distributions of proportion of fruit and animal matter in the diet of *C.mitis* throughout the species range.

4.4 Discussion

The intention of this chapter was to explore how samango monkey behavioural ecology, especially diet composition, varies across their large geographical distribution. The results of the study have shown that proportions of fruit, leaves and animal matter vary significantly between populations of samango monkey. There is a definite latitudinal pattern of increasing proportion of fruit in the diet towards the south, with increasing animal matter nearer the equator, and temperature seasonality appears to be the most important climatic variable in determining this variation. The ability for samangos to vary their diet depending upon the environmental conditions they encounter may be one of the leading contributing factors to their ability to survive further south than any other arboreal Cercopithecine species (Wolfheim 1982).

4.4.1 Fruit

As temperature seasonality increases there is an increase in the proportion of fruit in the diet of the monkeys. Temperature seasonality is negatively correlated with P.P.I. and since the original prediction was for proportion of fruit in the diet to increase with increasing P.P.I., this is a surprising result. This finding is opposite to a previous study investigating baboons, which showed a trend of increasing fruit feeding with increasing P.P.I. (Hill & Cowlishaw 2002). The most likely reason for this pattern is the negative correlation between proportion of animal matter in the diets of samangos and temperature seasonality. If both animal matter and fruit are "preferred" food options then in areas where they are both abundant it is likely to see them both present in samango diet. This would occur in areas of low temperature seasonality, which seems to be the case. Cercopithecines often consume relatively high amounts of invertebrates in their diets (Chapman et al. 2002); for example, diets of redtail monkeys (*Cercopithecus ascanius*) rarely compromise less than 20% insects (Chapman et al. 2002). Therefore, the result that in samango populations located where temperature seasonality is above 1°C, all diets contain less than 10% animal matter, indicates in those areas invertebrate food availability is likely to be low. As a result, in these high temperature

seasonality areas, where there is less animal matter in the diet, the samangos simply increase their fruit intake.

A second possible explanation for the decrease in proportion of fruit in the diet in less seasonal areas might be due to increased competition from other primate species in those more tropical areas. In the tropics there is a higher density of primate species when compared to more temperate areas (Wolfheim 1982, Eeley & Foley 1999) and many of these species will be competing for the available fruit. This may reduce access to fruit for the samango monkeys in these areas and so they are forced to find different food sources, i.e. animal matter.

4.4.2 Animal matter

The proportion of animal matter in the diet of samangos had a significant negative relationship with temperature seasonality and a significant positive relationship with P.P.I. Low temperature seasonality and high P.P.I. are associated with more tropical environments, so these results indicate that animal matter might be an important food source for samango monkeys at lower latitudes. P.P.I. is an indication of the potential growing season length of an area, and therefore, it stands to reason that an area with low P.P.I. is likely to have low primary productivity. Species richness for many animals increases in areas of high primary productivity (Currie 1991, Kay et al. 1997, Hawkins et al. 2003). P.P.I. also correlated significantly positively and temperature seasonality significantly negatively with mean annual precipitation at the samango study sites. Plant species richness is generally positively correlated with precipitation (Obrien 1993, Adler & Levine 2007) and increased plant diversity leads to a more diverse animal community (Hawkins et al. 2003, Novotny et al. 2006). Therefore, at sites where temperature seasonality is high and P.P.I. is low we might expect relatively low insect species richness. With fewer insect species it is perhaps not surprising that in areas of high temperature seasonality and low P.P.I. animal matter becomes a less important food source for samango monkeys in these areas.

In many locations non-aquatic insect species diversity decreases significantly during the dry season (Janzen & Schoener 1968, Wolda 1978). With dry periods taking up many months in highly seasonal areas, we would expect the amount of animal matter in the diet of samangos to decrease for at least part of the year for this reason, and this could go some way to explaining the pattern observed. This is supported by the significant positive correlation observed between proportion of animal matter in the diet and P.P.I.; indicating that in areas with long growing seasons and short or no dry season, the amount of animal matter in the diet increases.

4.4.3 Leaves

Guenons are characteristically frugivorous, but samangos monkeys are better adapted than other guenons for leaf consumption (Bruorton et al. 1991). The analyses conducted here showed no correlation between any climatic variables and proportion of leaves in the diet, although the proportion of leaves and fruit in samango diet had a strong negative relationship. This indicates that leaves may be a "fall-back" food which is used more in areas of lower fruit availability. In some studies leaf consumption is as high as 50% and it is perhaps this capacity for leaf consumption that allows samango monkeys to survive at lower latitudes than any other arboreal Cercopithecines (Wolfheim 1982). A previous analysis, showing leaves as an important dietary supplement during winter months in a southerly population, supports this hypothesis (Section 3.3.3). Therefore, a flexible diet may be the explanation for the large geographical distribution of the species, allowing them to survive in many different forest types (Kingdon et al. 2008c).

Generally the protein content of fruit is lower than that of leaves, especially young leaves (Milton 1981, Rogers et al. 1990, Oftedal 1991). In areas of low animal matter in their diet we might expect the monkeys would need to subsidise their diet with higher protein foods. However, this does not seem to be the case with samangos. In Ngoye, South Africa, Lawes et al. (1990) observed that the diet of the monkeys on site consisted of more than 80% fruit (84.4% in faecal analysis and 91.1% in an observational study). The monkeys there must be able to find

adequate protein in their diet and this shows that a sufficient amount of protein can be consumed even in a very high fruit content diet.

4.4.4 Dietary diversity

A high diurnal temperature range appears to be caused by a combination of low mean annual precipitation, high altitude and low temperature seasonality. Such areas would be expected to have lower primary productivity (Mohamed et al. 2004) and therefore potentially low species richness. Therefore, the close to significant relationship between diet diversity and diurnal temperature appears to be a conflicting one. The most likely explanation for this outcome is due to the combination of a low sample size (n=6) and the nature of the exploratory analyses being used causing the generation of Type I errors (Bland & Altman 1995a, Simmons et al. 2011). Although, due to the use of multiple tests, only relationships with an effect size of more than 0.5 were considered as significant (Nakagawa 2004), in this instance it appears that a low sample size may have contributed to this likely Type 1 error.

4.4.5 Conclusions

The ability for samangos to consume a more varied diet, often with a relatively high proportion of leaf material, than other arboreal guenons (Bruorton et al. 1991, Chapman et al. 2002) is potentially the main reason for their ability to occupy a more southerly range than any other African arboreal monkey (Wolfheim 1982). At times of climatic stress, when food availability may be scarce, they are able to supplement their diet with other foodstuffs (Rudran 1978, Lawes 1991). The results of the previous chapter indicated that during the winter months the samangos increased their overall food intake and the major contributor to this increase was leaf material. This further supports the suggestion that the ability for samangos to vary their diet allows them the potential to range further south, where there is higher temperature seasonality and lower overall temperatures (Hijmans et al. 2005). With the future of our climate currently uncertain, it is important to be able to predict how well certain species will be able to adapt to

different conditions. However, we should be careful in the way we interpret the results from such studies. It is unlikely that climatic variables are the only factors driving a species' behaviour and so in order to try to fully understand these aspects more data needs to be included, such as information on biotic interactions (Pearson & Dawson 2003).

The first two chapters presented here have investigated how variation in environmental factors, such as climate, can cause variation in the behavioural ecology of samango monkeys, both on a temporal and geographical scale. Resource variation is an important part of the foraging/risk trade-off, because for example, if resources are low an animal may be forced to take bigger risks to find food (Rasmussen 2005). The next three chapters investigate the other side of the foraging/risk trade-off, presenting detailed investigations of how variation in predation risk can cause samangos to considerably alter their behaviour, with potential long term consequences on their evolution.

Chapter 5

Landscapes of Fear

5.1 Introduction

Optimal foraging theory, first developed in the 1960s by MacArthur and Pianka (1966) and Emlen (1966), states that any organism will try to maximise its net energy intake per unit time. However, many factors limit an animal's ability to optimise foraging behaviour, including competition and predation (Kotler & Holt 1989). For example, many species must remain visually vigilant for threats in order to minimise their negative effects, but few species are able to feed and remain vigilant at the same time (Treves 2000). Alternatively, preferred food sources might be located in high risk habitats (Ylönen et al. 2002). Therefore, many animals are often forced to trade-off time spent foraging and the consequent increase in risk associated (Werner & Anholt 1993, Lima 1998).

5.1.1 Landscapes of fear

The risk of predation varies with environmental factors such as the degree of cover provided by vegetation, or the accessibility of an area to predators, such as a cliff face as opposed to open grassland (Mcnamara & Houston 1987, Lima 1998, Brown & Kotler 2004). These factors allow for the construction of a "landscape of fear" indicating spatially where a prey species perceives higher predation risk (Laundre et al. 2001). The landscape exists because different features of a prey's environment may offer lesser or greater advantages to a predator (van der Merwe & Brown 2008). Visualising these landscapes allows great insights into the factors which drive animal movements and spatial ecology.

Most of the empirical work investigating landscapes of fear has been conducted with non-primate species. For example, Hernandez & Laundre (2005) used

landscapes of fear to show that when wolves were re-introduced to some areas of Yellowstone National Park, the elk resident there shifted their space use to areas closer to woodland, which provided better protection. Similarly, van der Merwe & Brown (2008) mapped the landscape of fear of the Cape ground squirrel (*Xerus inauris*) and showed that spatial use was limited by predation risk with squirrels preferring areas of close proximity to burrows and with open sight lines. More recently landscapes of fear have been constructed for species such as Nubian ibex (*Capra nubiana*) (Iribarren & Kotler 2012), desert cottontail rabbit (*Sylvilagus audubonii*) (Arias-Del Razo et al. 2012) and black-tailed jackrabbit (*Lepus californicu*) (Arias-Del Razo et al. 2012). These studies show how the landscape of fear is an idea currently at the forefront of ecology. So far this concept has been little applied to primates and yet primates, because of their varied and specific predator responses, make excellent model species for the study of spatial variation in predation risk.

5.1.2 Behavioural landscapes of fear

The majority of monkey species have predator alarm calls and for many species these vocalisations are predator-specific (e.g. Seyfarth et al. 1980, Ferrari & Ferrari 1990, Zuberbuhler et al. 1997). These alarm calls provide an excellent tool for assessing spatially perceived predation risk. In one of the first studies to produce a utilisable probabilistic landscape of fear, Willems and Hill (2009b) investigated predator-specific landscapes of fear in vervet monkeys by recording the location of vervet alarm calls in their home range. Struhsaker (1967a) first noted that vervet monkeys give acoustically different alarm calls in response to the threat from different predators, with each call invoking different anti-predator behaviours. Willems and Hill (2009b) were able to construct detailed landscapes of fear that were predator-specific based on these varied vocalisations (Figure 5.1). They found that chacma baboon and leopard fear caused the monkeys to avoid areas where the risk of predation was perceived to be high (Figure 5.2). These effects on ranging were stronger than the overall effect of food availability. Eagle and snake risk had no significant effect on vervet ranging behaviour. The lack of an eagle effect was attributed to the fact that eagles are often detected at a

distance and a better response is to move vertically downwards and find cover, rather than a horizontal movement change. The lack of a snake effect was attributed to the fact that most snakes on site were not true predators of the vervet monkeys. Nevertheless, these results provide strong support for spatial variation in predation risk operating as a powerful selective force on primate behaviour and highlight the need to assess effects of multiple predators on the behaviour of prey (see also Shultz et al. 2004). One of the conclusions from the study was the potential to incorporate other factors that could affect space use, such as inter-group competition, visibility and height of trees. No study has yet investigated the simultaneous effects of such a number of different factors on space use.

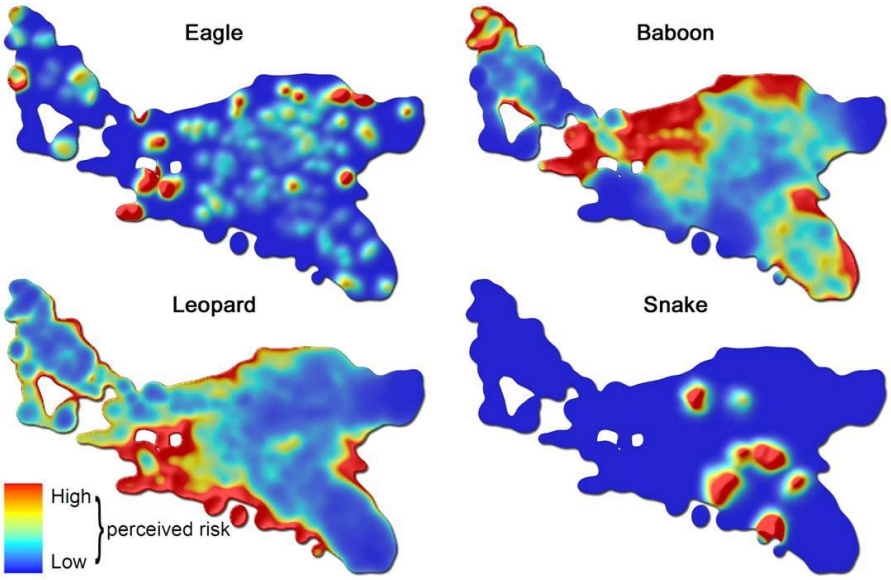

Figure 5.1 "*Landscapes of fear*" of the Willems & Hill (2009) vervet monkey study group, for four different potential predators. Landscapes are created by mapping the locations of predator-specific alarm vocalisations and taking into account utilisation distribution (Figure 5.2). The landscapes are therefore a representation of spatially perceived predation risk.

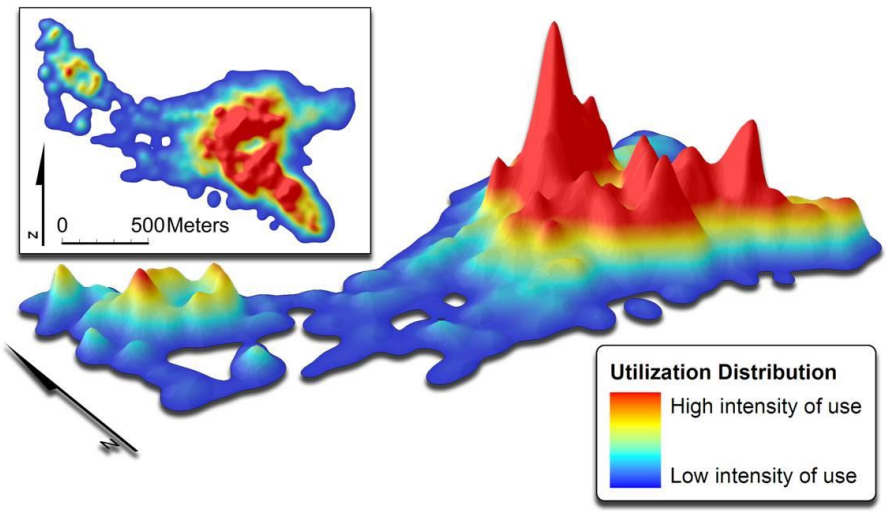

Figure 5.2 Home range area of the Willems & Hill (2009) vervet monkey study group (114ha), showing the intensity of space use (utilisation distribution).

5.1.3 Predation risk in samango monkeys

Samangos, as an arboreal monkey species, may suffer different predation threats to more terrestrially adapted species (Lawes 1991, McGraw 2002). In a study of crowned eagles Mitani et al. (2001) observed that eagles were more likely to attack arboreal redtail monkeys rather than the more terrestrial grey-cheeked mangabeys (*Lophocebus albigena johnstoni*). A second study in the Ituri Forest, Democratic Republic of Congo, found that based on their overall density in the forest, terrestrial primates were overrepresented and arboreal primates underrepresented in leopard and golden cat (*Felis aurata*) diets (Hart et al. 1996). Several other studies have shown raptors as significant predators of arboreal monkeys (e.g. Struhsaker & Leakey 1990, Miranda et al. 2006, Fam & Nijman 2011) and a number of studies have reported eagle predation on samango monkeys (Brown 1971, van Jaarsveld 1984, Skorupa 1989, Struhsaker & Leakey 1990, Cordeiro 2003), confirming them as likely predators of the samangos at Lajuma. In the Tai Forest, Ivory Coast the mean prey weight for crowned eagles was 5.67 ± 3.33kg. Adult samangos, both male and female are generally found within this weight range (Mean ♀ weight 4.4kg, mean ♂ weight 7.6kg (Harvey et al. 1987). However, a conflicting result from Shultz et al (2004) showed that eagles in the Tai National Park, Ivory Coast showed no preference for either arboreal or terrestrial primates. Nevertheless, collectively the studies mentioned suggest that

as arboreal monkeys, samangos may suffer a higher risk from raptors than more terrestrial predators.

Samango monkeys have evolved a number of anti-raptor behaviours. Perhaps the most apparent of these is an eagle-specific alarm vocalisation, which many studies have identified as a "ka" or "ka-train" call, given only by adult males (Cords 1987, Brown 1989, Macleod 2000, Cordeiro 2003, Papworth et al. 2008). Studies have suggested that a common response upon hearing this alarm call is for members of the group to move vertically down in the canopy (Cords & Rowell 1987, Macleod 2000, Cordeiro 2003). Some studies have also suggested that male samangos will sometimes aggressively challenge an eagle perching in the canopy (Brown 1971, Macleod 2000, Cordeiro 2003), though a large eagle poses a significant mortality threat even to an adult male samango (van Jaarsveld 1984, Struhsaker & Leakey 1990). All of the studies mentioned suggest that the potential risk to samangos at Lajuma is high, this could lead to the samangos avoiding areas they consider a high risk of eagle predation.

Only one study has identified a leopard-specific samango alarm call, from playback experiments with groups in Budongo Forest, Uganda (Papworth et al. 2008). They reported that the adult male "pyow" call was used; a call never previously reported in this context (Marler 1973, Cords 1987). Aldrich-Blake (1970) suggested that such loud male vocalisations usually function for maintaining inter-group spacing and/or territorial defence. Therefore, the Papworth et al. (2008) study presents an interesting possibility for a potential leopard-specific alarm call. Previous studies have shown that the samangos on site consider the understory a high predation risk area (Emerson et al. 2011, Gaynor & Cords 2012) and this risk is most likely to come from terrestrial predators (Struhsaker 1967b, Hart et al. 1996) such as leopards (Willems & Hill 2009b). Leopards are known to feed on the samangos on site, although samangos only comprise 2.1% of their diet (Chase-Grey 2011). Therefore, it is expected that, similarly to vervet monkeys, the samangos will avoid areas they consider a high risk of leopard predation.

5.1.4 Inter-group competition

Inter-group competition has the potential to significantly affect range use, especially in a territorial species. A group may attempt to avoid inter-group encounters due to the mortality/injury risk posed predicting that areas of high risk of encounter should be avoided (Chapman 1990, Gibson & Koenig 2012). Alternatively a group might look to defend their territory against rival groups and so may spend increased time patrolling areas of high inter-group encounter risk (Lowen & Dunbar 1994). Grey-cheeked mangabeys have been shown to avoid areas towards the edge of their home ranges and try to actively avoid inter-group encounters (Barrett & Lowen 1998). Garber et al. (1993) showed that moustached tamarins show no evidence of patrolling borders; whereas, Lledo-Ferrer et al. (2011) observed that saddleback tamarins spend significant periods of time scent marking around the edges of their home ranges. These studies show the potential variability the effect of inter-group encounters risk may have on a group of territorial monkeys and that further research is clearly required. Samangos are a territorial species often engaging in aggressive inter-group encounters (Lawes & Henzi 1995). Therefore, risk of these encounters has the potential to significantly affect their ranging behaviour, although it is difficult to make predictions in this regard.

5.1.5 Environmental factors

Primates will attempt to spend as much time as possible in areas of high food availability (Schoener 1971), although there is often a foraging/risk trade-off to consider (Lima 1988). It is also highly likely that an arboreal monkey species would avoid areas of low mean canopy height (Enstam & Isbell 2004). Sichuan snub-nosed monkeys have been shown to spend >94% of their time in trees over 6m tall (Li 2007). Similarly black howler monkeys (Pozo-Montuy et al. 2011) and patas monkeys (*Erythrocebus patas*) (Enstam & Isbell 2004) have been shown to prefer areas of taller canopy. In the Ituri Forest, Democratic Republic of Congo, samango monkeys have been observed to spend the majority of their time above 10m (Thomas 1991) and utilising giving up density experiments Emerson et al. (2011) observed that samangos at Lajuma considered higher risk of predation to

be close to the ground. Therefore, it is expected that the samangos would prefer areas of taller canopy.

A habitat with high foliage density may provide cover from a predator but may limit an individual's ability to monitor its surroundings; whilst high visibility may have the opposite effect. Areas of high foliage density will tend to have low visibility which may hinder a predator's movement (Boinski et al. 2003) or may provide camouflage from potential predators (Tchabovsky et al. 2001). However, areas of high visibility may increase an individual's ability to monitor threats from predators or competitors (Cowlishaw 1994, Hill & Weingrill 2007, Jaffe & Isbell 2009). For example, vervet monkeys have been shown to decrease vigilance in high visibility areas (Chapman 1985, Enstam & Isbell 2002). This suggests a reduction in perceived risk, although range use was not investigated in these studies. The studies mentioned suggest the most likely response for samangos is a preference for areas of high visibility, due to the improved ability to remain vigilant in these areas.

5.1.6 Objectives

Many previous primate studies have attempted to explain ranging behaviour purely using data on resource distribution (Schoener 1971, Mitani 1989, Fridell & Litvaitis 1991, Mitchell & Powell 2007), failing to take into account that the risk of predation tends to vary, sometimes quite dramatically, over space (Brown & Kotler 2004). This study provides an original investigation of how perceived predation risk, risk from rival groups and a number of specific environmental factors can affect the movements of an arboreal monkey species. Understanding the overall effect of such factors can give us great insights into the movement ecology of arboreal monkeys, something never previously attempted with such a species. Based on the results of previous studies a number of predictions have been formed:

1) Samangos will avoid areas of high perceived eagle and leopard predation risk.

2) Samangos will prefer areas of higher canopy, high food availability and high visibility.

5.2 Methods

5.2.1 Study site

Research was conducted at the Lajuma Research Centre, located in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). Substantial local variation in abiotic factors such as elevation and water availability result in a variety of microclimates which are able to support a substantial diversity of both flora and fauna (Brock et al. 2003, Willems 2007). The area has natural areas of tall forest (10-20m height) occurring amongst areas of natural short forest (5-10m height). These are interspersed by areas of bushveld (<5m height) resulting from disturbance. For a detailed description of the site see Section 2.2.

All five southern-African non-human primates are resident in abundance. Along with samango monkeys, these are the vervet monkey, chacma baboon, thick-tailed galago and southern lesser bushbaby. The most notable potential predators include leopard, crowned eagle, African black eagle and the African rock python. Furthermore, venomous snakes, whilst not actively preying on samangos, still pose significant mortality threats and may therefore affect range use. Common species include black mamba, puff adder and the Mozambique spitting cobra.

5.2.2 Study species

Samango monkeys are primarily frugivorous (Lawes 1991), medium sized, arboreal guenons, which form single-male, multi-female groups with group sizes ranging from 4-65 (Butynski 1990, Beeson et al. 1996, Smith et al. 2008, Houle et al. 2010, Lawes et al. 2011). Samangos have a variety of vocalisations, with a number classed as alarm vocalisations. These include an alarm call which has been

well documented as referentially specific to aerial threats such as raptors (Brown 1989, Papworth et al. 2008) and in one study in Uganda, a leopard-specific alarm call has been observed (Papworth et al. 2008).

5.2.3 Data collection

A habituated samango group of approximately 40 individuals were observed over a 16 months period, with data collection occurring over the last 12 months (Jan-Dec 2010). Behavioural data collection consisted of eight successful follow days per month (totalling 96 days), with a successful day consisting of following the group from dawn to dusk without losing audiovisual contact for more than a total of 60 minutes. Study days ranged approximately 11.5-13.5 hours depending upon season.

5.2.4 Utilisation distribution

The utilisation distribution was the same as used in Chapter 3. This was created using 6912 locational data points representing 10 minute periods, and then adaptive LoCoH analysis was used to calculate intensity of space use (Figure 5.3). For a more detailed description of the LoCoH method see Section 2.5.3.

5.2.5 Environmental parameters

Habitat type

The monkey home range was separated into eight distinct habitat types: tall forest; short forest; riverine forest; wetland; open/closed mountain bushveld and open/closed rocky mountain bushveld (Figure 5.4, based on criteria in Musina & Rutherford 2006; for a more detailed explanation of the habitat types see Section 2.4.3)

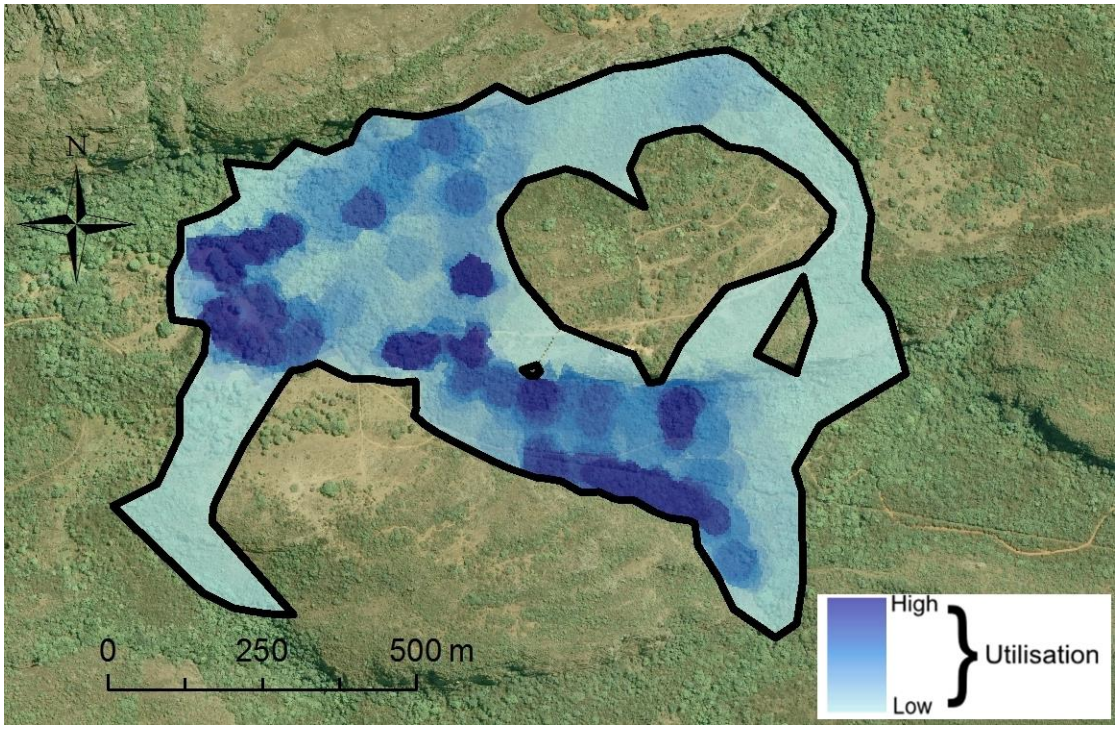

Figure 5.3 Home range and utilisation distribution of the study group (54.7ha) constructed using Adaptive LoCoH analysis. The black outline indicates the edges of the home range. Dark blue areas indicate areas of high utilisation and light areas indicate low utilisation. The home range is overlaid on a satellite image of the study site.

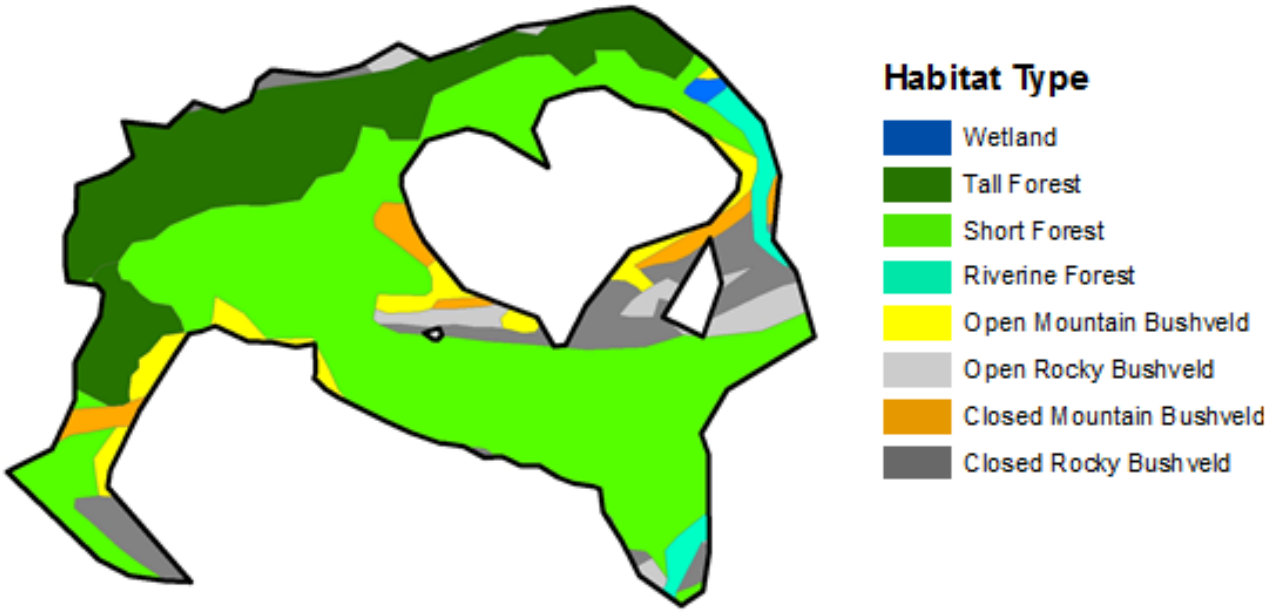

Figure 5.4 Locations of the eight habitat types found within the monkey home range.

Food availability

Food availability was calculated with data from phenological transects and randomly placed quadrats (see Section 2.5.2). Fruit was the dominant food type in the diet of the study group contributing 51.7% of adult feeding time (based on scan data). Therefore, using eight of the most eaten tree species (see Table 2.10), a figure for total number of fruits in each $25m^2$ quadrat was calculated (a total of 1268 quadrats over the 12 months data collection period). In the quadrats only trees with a circumference ≥0.1m at a height of 1m were included. Fruit size was accounted for in each species to obtain a total fruit volume measurement per quadrat. This was achieved by estimating an average fruit size for each species (based on measurements in Coates-Palgrave 1996; *Acacia* pods were given a nominal thickness of 1mm) (Table 2.11). Average fruit availability per $25m^2$ quadrat was calculated for each habitat type. This fruit availability calculation was used to represent food availability in the analyses.

Canopy height

Using the same quadrat data as above, a mean canopy height per $25m^2$ was calculated for each habitat type. In the quadrats for trees below 5m tall a tape measure was used to measure height; for trees above 5m height was estimated.

Visibility

On a bimonthly basis, at each quadrat site, a percentage understory visibility measurement was estimated using a 10 x 10 ($0.64m^2$) grid held at a height of two metres at each of the four cardinal points and at a distance of five metres (total 632 sites). From these four measurements an average visibility per $25m^2$ was calculated. Visibility measurements using this method at a height of more than two metres were not feasible in the terrain, therefore all data is a measurement of understory visibility.

Landscapes of fruit availability, canopy height and visibility measurements

To investigate the overall effect of the environmental parameters, landscapes of fruit availability, canopy height and understory visibility were constructed (Figure 5.5). The average fruit availability/canopy height/visibility per $25m^2$ quadrat

were interpolated using kriging (Cressie 1990) in ArcGIS. The search radii for the kriging were calculated based on the number of points achieving minimum root mean squared error (Food = 45, Canopy Height = 45, Visibility = 60) (Salih et al. 2002).

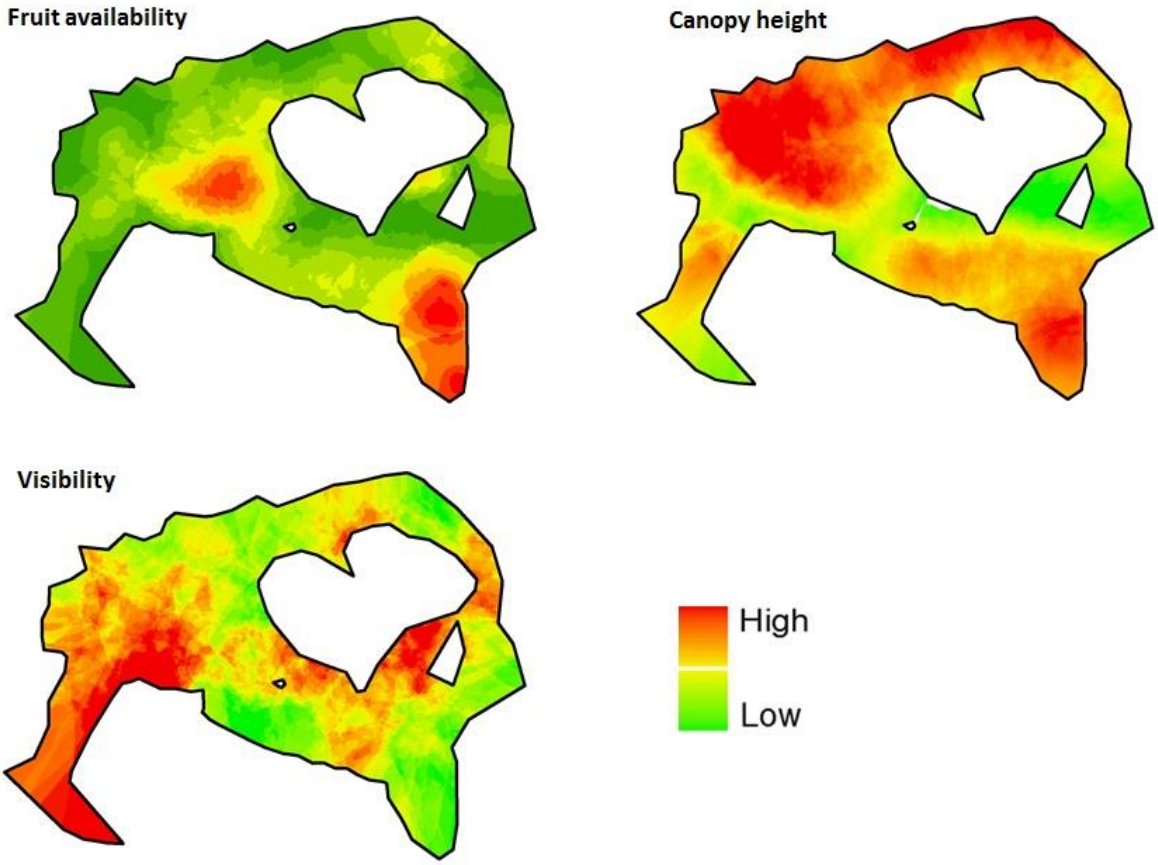

Figure 5.5 Maps showing fruit availability, canopy height and understory visibility after interpolations using kriging.

Sleeping sites and water availability

The locations of sleeping sites were recorded using the final GPS location of the day. Water sources were counted as sources of water available for a minimum of one month and their locations were recorded using GPS. To determine their distribution in the landscape these factors were expressed using Euclidean distances calculated using ArcGIS (Figure 5.6).

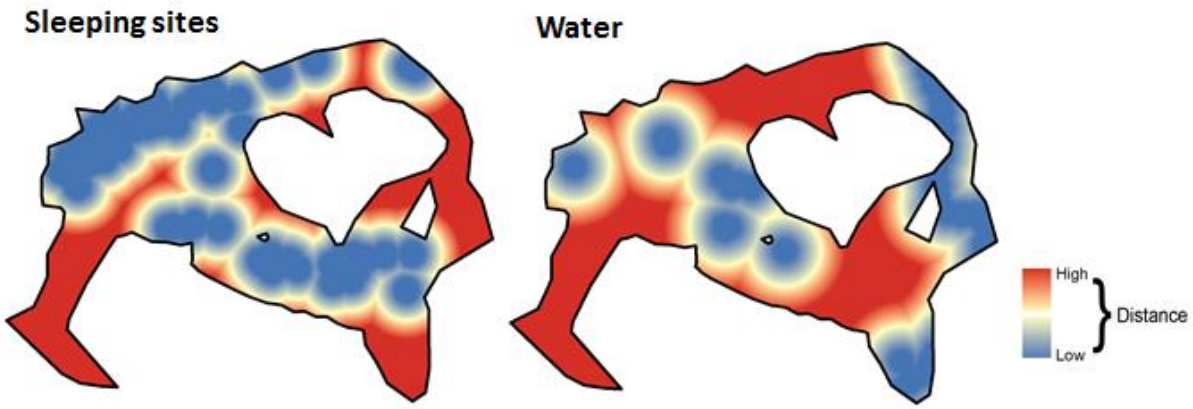

Figure 5.6 Euclidean distances of sleeping sites and water sources in the monkey home range.

5.2.6 Landscapes of fear

Samango monkeys have evolved distinct alarm calls which can be easily disseminated by human observers (Brown 1989, Papworth et al. 2008). Arboreal monkeys, such as samangos, pose certain difficulties to an observer; mainly the difficulty of observation in tall trees or dense canopy. However, the use of alarm calls to measure perceived predation risk allows for data to be collected without a direct line of sight of the target individual. During this study the only predator-specific alarm call identified was the eagle call, defined as a series of "kas" and "ka-trains" by the adult male. Other alarm calls to be counted predator-specific needed to be accompanied by visual verification of the predator species. Total alarm calls were categorised as follows: eagle=59, snake=3, other=7, unknown=62. There were no observed leopard-specific alarm vocalisations. Of the 59 eagle alarm calls only 11 were accompanied by an eagle sighting, leaving 48 potentially "false" alarm calls. These calls, however, still express the monkeys' perception of eagle risk and are therefore just as informative as when an eagle was sighted. A minimum of 10 locational observations are required for the statistical techniques used (Borger et al. 2006), so only eagle alarm calls could be investigated. The locations and details of all inter-group encounters were recorded (Figure 5.7). An inter-group encounter was defined as visual fixation of the competitor group by at least one member of the study group. In total there were 41 inter-group encounters of varying antagonism during the study period.

Fixed kernel density estimation with a PLUGIN bandwidth parameterisation was employed to create a density distribution of the eagle alarm vocalisations and inter-group encounters (Figure 5.8). The often favoured LSCV bandwidth appreciably over smoothed the distributions and on smaller samples PLUGIN has been shown to have less variability and outperform LSCV (Gitzen et al. 2006, Lichti & Swihart 2011). With sample sizes of 59 (eagle alarm calls) and 41 (inter-group encounters) PLUGIN was chosen as the best bandwidth option. Finally in ArcGIS the landscapes of fear and competition were created by dividing the kernel density estimation (Figure 5.8) by the utilisation distribution (Figure 5.3) generating a map detailing risk spatially throughout the monkey home range.

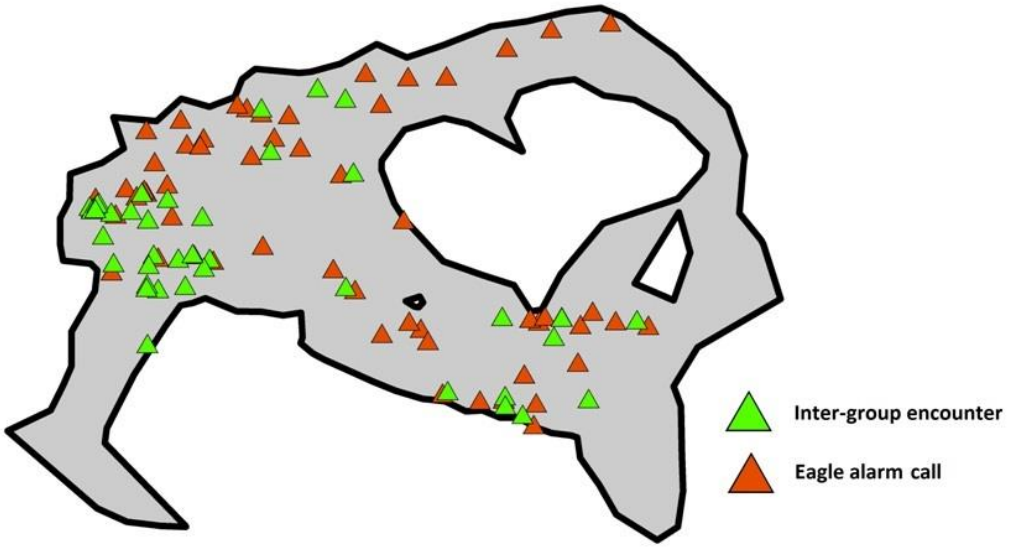

Figure 5.7 Locations of all eagle alarm calls and inter-group encounters within the monkey home range.

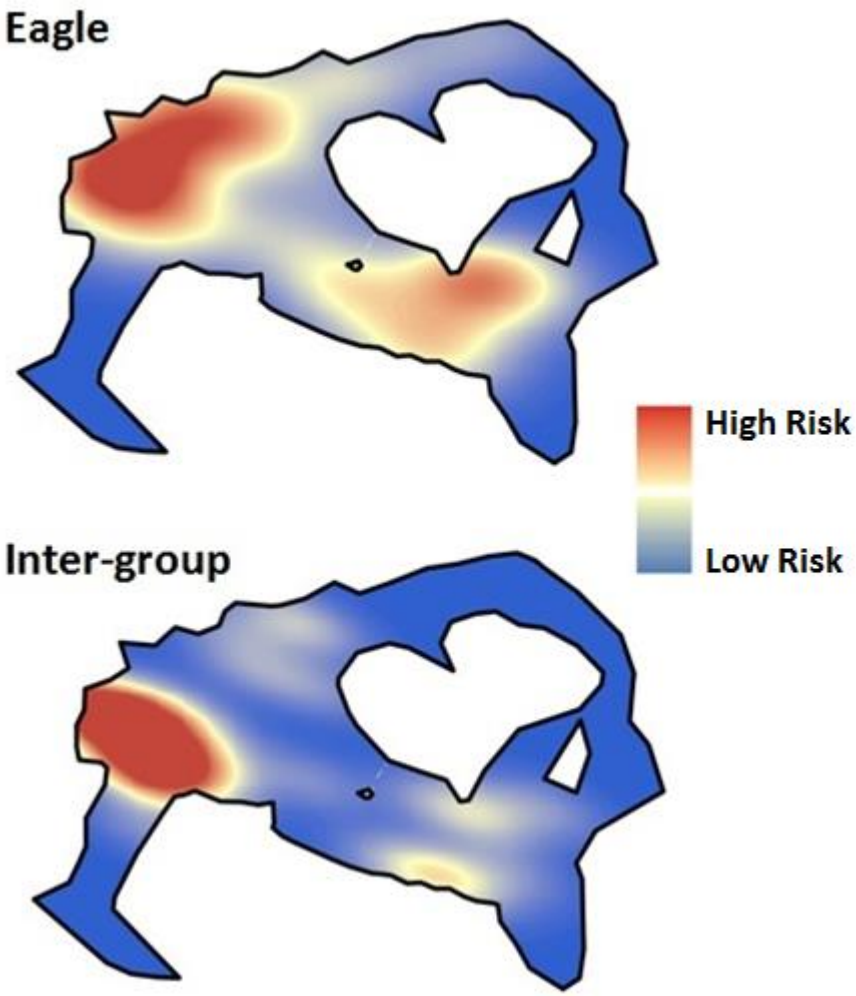

Figure 5.8 Kernel density estimations based on eagle alarm calls and inter-group encounters.

5.2.7 Statistical analysis

A random set of 1000 points within the monkey home range were selected, using Geospatial Modelling Environment (Version 0.5.5 Beta, Hawthorne L. Beyer, 2011). Attached to each of these points was information detailing levels of all the environmental parameters and data from the landscapes of eagle fear and inter-group encounters at that specific location. Spatial autocorrelation is often a problem when analysing spatially variable ecological data, potentially substantially increasing the risk of Type I errors (Dormann et al. 2007). The spatial patterns within these data were assessed by inspection of correlograms and Moran's *I* values (Figure 5.9). A Moran's *I* figure around ±1 signifies strong

positive/negative autocorrelation; a figure close to 0 means no autocorrelation (Ripa 2000). To account for spatial autocorrelation within the variables exploratory Pearson's correlation analyses with adjusted degrees of freedom (Dutilleul 1993) were used.

To determine the overall effect of each of the predictor variables on the intensity of space use simultaneously, whilst also accounting for spatial autocorrelation, two mixed regressive-spatial regressive (or lagged predictor) models were used following Willems and Hill (2009b). Model A mirrored the model used by Willems & Hill (2009b) using dummy coded habitat types and included perceived eagle predation risk, distance from water and sleeping sites as separate predictor variables. The eight different habitat types were recoded into seven dummy variables (with wetland used as the reference category). In order to investigate the effect of habitat variables in more detail and the effect of inter-group encounters a second mixed regressive-spatial regressive model (Model B) was used. The habitat types were broken down into their constituent parts of fruit availability, canopy height and understory visibility; all interpolated from the kriging analyses and used as separate predictor variables. A measurement for inter-group encounter risk was also included as a predictor variable in the analysis. Models were selected based on the two-step procedure suggested by Richards (2008). To begin with all models with an AIC number within 6 of the model with the smallest AIC number (ΔAIC) were selected. Next, to remove overly complex models, any models which had a higher AIC value than any simpler nested model were disregarded. Visual inspection of the residuals from the models confirmed the data were close to normally distributed (Figure 5.10). Analyses were conducted using the package Spatial Analysis in Macroecology and global Moran's *I* statistics were calculated in ArcGIS

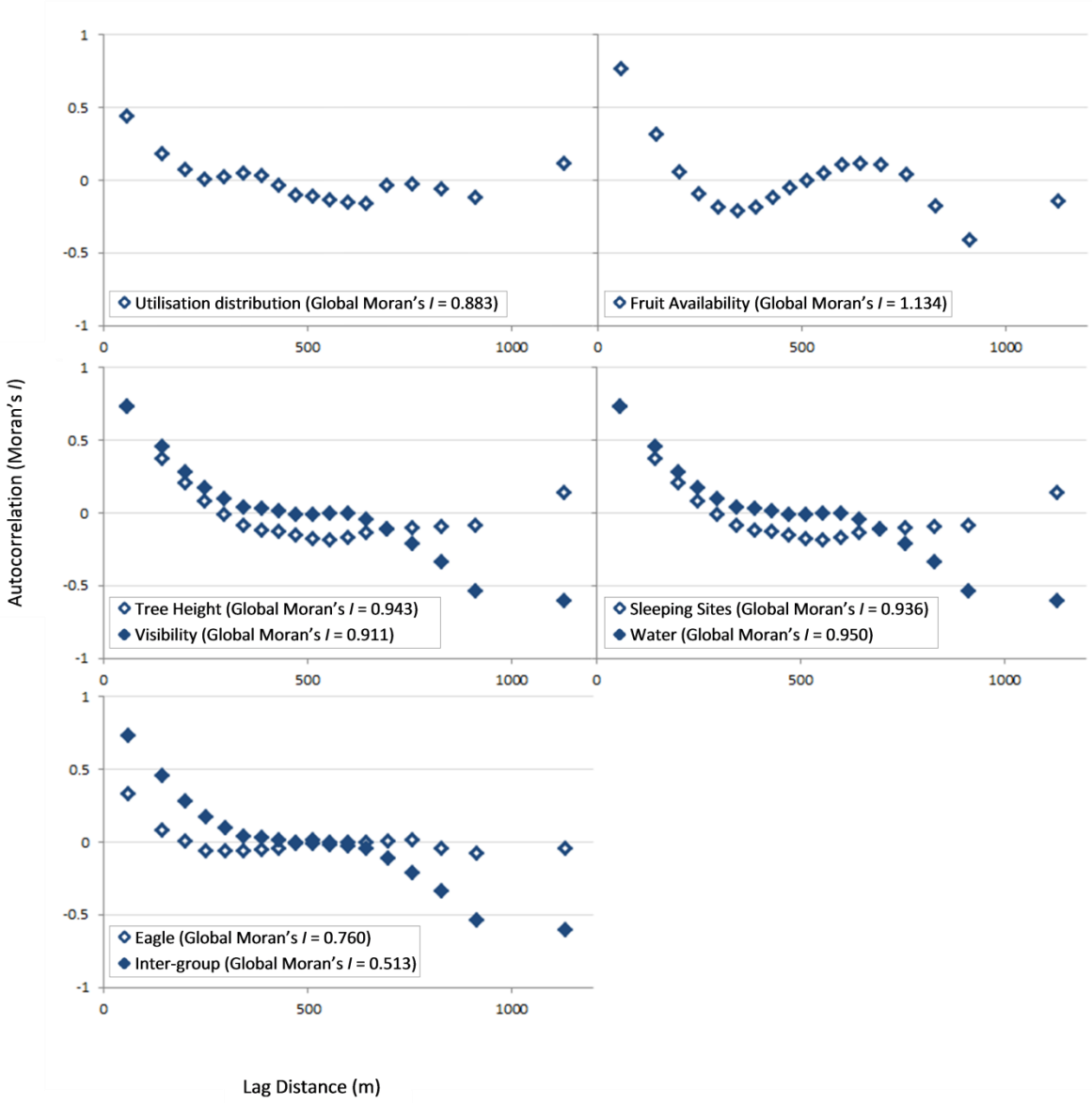

Figure 5.9 Correlograms and global Moran's *I* values indicating level of spatial autocorrelation within all variables. Global values were calculated in ArcGIS.

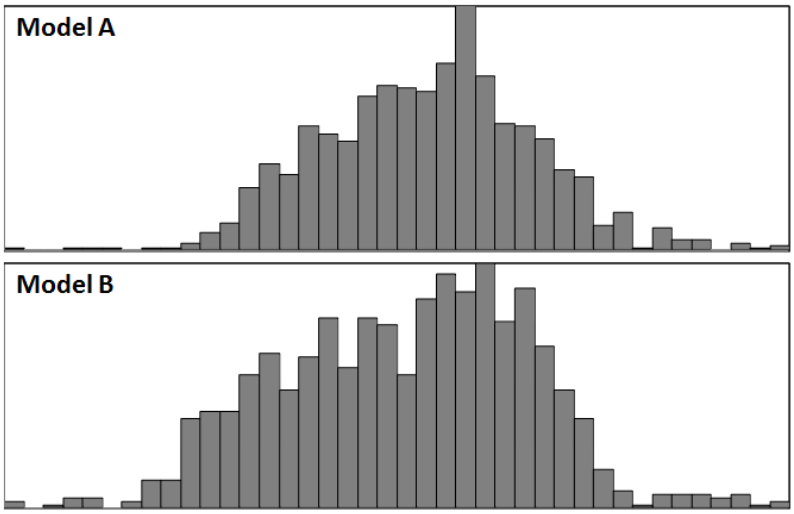

Figure 5.10 Residual distributions from the spatial regressive-mixed regressive models. Model A skewness = .018, excess kurtosis = .274. Model B skewness = -.103, excess kurtosis = -.211. A rule of thumb for skewness or excess kurtosis is a score of more than ±1 is considered strongly non-normally distributed (Fife-Schaw et al. 2006).

5.3 Results

5.3.1 Landscapes

The landscapes of eagle risk (Figure 5.11) indicate a few areas of high perceived eagle risk centred mostly around the north-western and eastern portions of the samango home range. The landscape of inter-group encounters (Figure 5.12), indicates that the highest levels of inter-group encounter risk were centred around the western portion of the home range.

5.3.2 Linear correlation analysis

Significant negative relationships exist between the home range utilisation distribution and perceived predation risk and distance to sleeping sites, with the strongest relationship with the eagle landscape of fear (Table 5.1). No other factor had a significant relationship with intensity of space use in this univariate analysis.

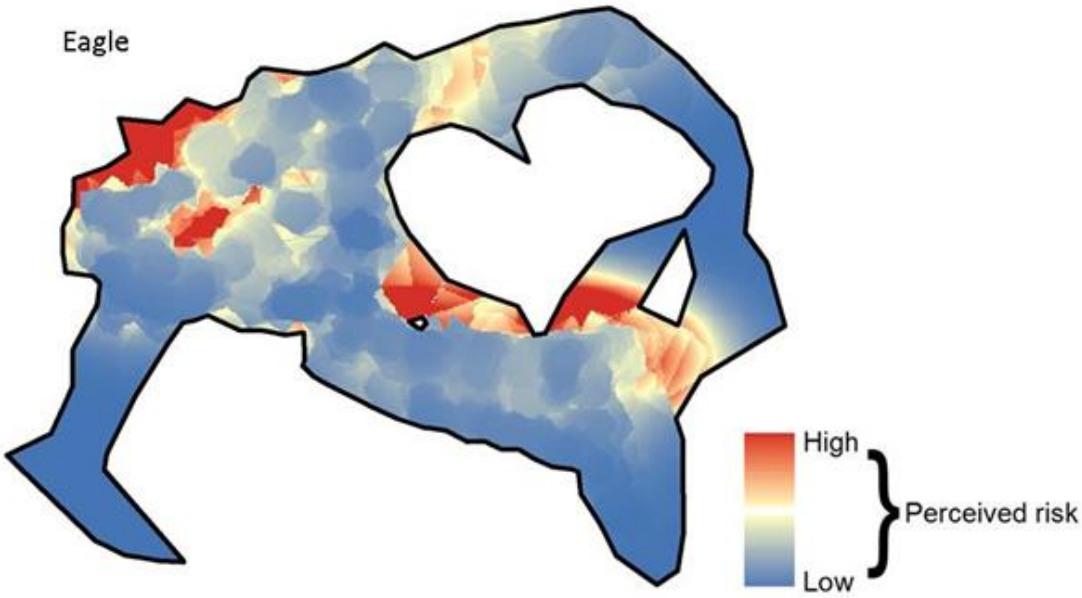

Figure 5.11 Representation of perceived eagle predation risk.

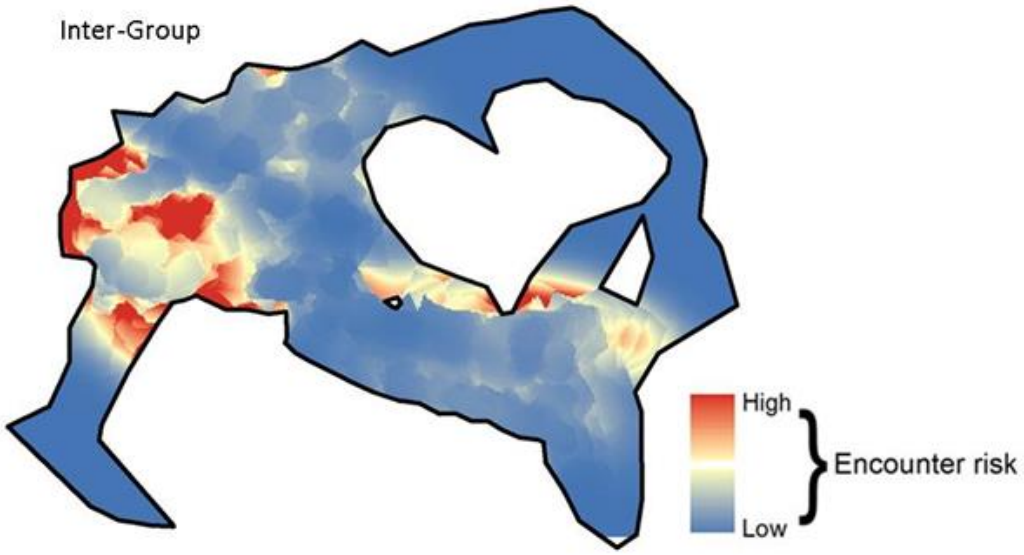

Figure 5.12 Representation of inter-group encounter risk.

Table 5.1 Results of Pearson's correlation analyses (*n*=1000) based on geographically corrected degrees of freedom (Dutilleul 1993) between the utilisation distribution and perceived predation risk, inter-group encounters and other environmental parameters. Statistically significant (p = <.05) are highlighted in bold.

Predictor	Pearson *r*	Corrected *df*	p
Landscapes of fear			
Eagle	-.277	98.667	**.005**
Inter-group	-.063	84.162	.563
Environmental factors			
Fruit availability	.120	44.606	.423
Understory visibility	-.102	38.631	.529
Height of trees	.138	32.017	.435
Sleeping sites	-.410	33.353	**.014**
Water availability	-.218	46.484	.134

5.3.3 Spatial regression analysis

Two mixed regressive-spatial regressive (lagged predictor) models were used in order to determine the extent to which the variation in intensity of space use could be ascribed to the simultaneous effects of all the other investigated variables. Model A, containing the different habitat types, indicated significant negative relationships between range use and both perceived eagle predation and distance to sleeping sites (Table 5.2). The model shows that the tall forest was preferred by samangos over all other habitat types, whereas riverine forest, open and closed mountain bushveld and open and closed rocky mountain bushveld were all significantly avoided. These results are contrary to what would be expected on the basis of habitat food availability, with open mountain bushveld, closed rocky bushveld, and short forest all containing a higher mean fruit availability than tall forest (Table 5.3). Hence, the preference for tall forest might suggest a selection for canopy height. Water availability was dropped from the model following AIC selection, indicating no important effect on range use. According to this model the strongest predictor of range use was the negative effect perceived eagle predation risk

Table 5.2 Results from Model A, a mixed regressive-spatial regressive model, with the response variable utilisation distribution vs. perceived eagle predation risk, habitat types and distance to sleeping sites. Habitat types are presented in descending order of fruit availability. Other model statistics: n=1000; R^2=.312; ρ=±.172, AIC_c=8046.8. Terms: γ, spatial cross-regressive parameter; β, unstandardised regression parameter; B, standardised regression parameter; ρ, spatial autoregressive parameter. Statistically significant results (p = <.05) are highlighted in bold.

Predictor	β	B	SE B	γ	SE γ	t (β=0)	p
Landscape of fear							
Eagle risk	-.329	-.338	.028	.992	.192	-11.583	**<.001**
Habitat types							
Short Forest	.018	.018	.038	.992	.171	.476	.635
Open Mountain	-.092	-.121	.022	.992	.518	-4.158	**<.001**
Closed Rocky	-.233	-.289	.024	.992	.408	-9.796	**<.001**
Tall Forest	.091	.083	.046	.992	.118	1.998	**.046**
Closed Mountain	-.095	-.138	.019	.992	.758	-4.989	**<.001**
Riverine	-.162	-.211	.022	.992	.495	-7.369	**<.001**
Open Rocky	-.132	-.19	.02	.992	.736	-6.538	**<.001**
Environmental factors							
Sleeping sites	-.353	-.154	.063	.992	.006	-5.582	**<.001**

Table 5.3 Mean canopy height, fruit volume per 25m^2, and understory visibility in the eight habitat types found in the monkey home range.

Habitat	Mean Canopy Height (m)	Mean Fruit Volume (cm^3)	Mean Visibility (%)
Tall Forest	5.58	10350	58.45
Riverine Forest	5.82	6261	59.65
Short Forest	5.01	14977	56.41
Closed Mountain	4.96	10072	66.70
Open Mountain	3.72	13358	63.22
Open Rocky	3.95	3680	49.94
Closed Rocky	3.77	12677	58.68
Wetland	3.91	12675	56.31

For Model B the habitat types were broken down into separate measurements for food availability, understory visibility and canopy height (Table 5.4). Similar to the first model, perceived eagle predation risk and distance to sleeping sites showed negative relationships with utilisation. Canopy height and visibility had positive relationships with range use, suggesting that the monkeys prefer areas of high trees and high visibility. Within these the two strongest predictors of range use are perceived eagle predation risk and canopy height. Based on AIC selection, inter-group encounters, water availability and fruit availability were dropped from the model, indicating no important effects on range use.

In an attempt to understand the lack of effect on space use of fruit availability in the second model a third mixed regressive-spatial regressive model was utilised. Fruit availability was used as the response variable, with canopy height and understory visibility as the predictor variables. The results from this analysis show that high fruit availability tends to be in areas of high canopy height and low visibility (Table 5.5). Therefore, the lack of effect on range use from fruit availability might be a result of the significant effects of canopy height and visibility.

Table 5.4 Results from Model B, a mixed regressive-spatial regressive model, with the response variable utilisation distribution vs. perceived eagle predation risk and other environmental factors. Other model statistics: n=1000; R^2=.169; ρ=.992±.172, AIC_c=8215.3.

Predictor	β	B	SE B	γ	SE γ	t (β=0)	p
Landscapes of fear							
Eagle	-.271	-.278	.029	.992	.192	-9.322	**<.001**
Environmental factors							
Understory visibility	.173	.109	.048	.992	.027	8.838	**<.001**
Height of trees	.398	.277	.045	.992	.041	-3.561	**<.001**
Sleeping sites	.334	-.146	.071	.992	.006	-4.720	**<.001**

Table 5.5 Results of a mixed regressive-spatial regressive analysis with fruit availability as a function of height of trees and understory visibility. n=1000; R^2=.057; ρ=.992±.04; AIC_c=20938.2

Predictor	β	B	SE B	γ	SE γ	t (β=0)	p
Height	.053	.061	.027	.992	.072	1.989	**.047**
Understory visibility	-.190	-.236	.025	.992	.094	-7.659	**<.001**

5.1 Discussion

This study is the first to quantify spatially variable predation risk and investigate how this, and the distribution of a range of environmental factors, affects the range use of an arboreal monkey species. The results of the analysis have shown that perceived eagle predation risk is one of the most important factors driving samango monkey space use. This effect was stronger than any of the environmental variables investigated, including food availability which had no observable effect on samango space use. The results of this study and those of Willems & Hill (2009b) allow for a detailed comparison between an arboreal and a semi-terrestrial monkey species living within the same location. This provides important insights into how two primate species, sharing similar niches, vary in their behavioural ecology.

5.4.1 Eagle predation risk

Eagle predation risk had a strong negative association with samango monkey space use. This suggests that the eagles posed such a threat that the samangos avoided areas they considered high risk, which would otherwise be beneficial for them to spend time in. This is contrary to data on the vervet monkeys on site which showed no significant relationship between eagle risk and vervet ranging behaviour (Willems & Hill 2009b). Willems and Hill (2009b) attributed the lack of eagle response from the vervets to there being a constant level of eagle predation

risk throughout the home range, due to the eagles' ability to occupy large hunting areas and to spot prey from a distance. However, previous studies have noted that many eagles prefer to hunt from a perched position high in the canopy, especially in areas of relatively dense vegetation or high density of prey species (for example Hancock 1964, Garrett et al. 1993, Scheller et al. 2001, Shultz 2001, Valdez & Osborn 2004). If this is the case for the eagles in Lajuma then there should be areas of high eagle predation risk where the eagles are choosing perch hunting and the results from this study seem to be compatible with this hypothesis. The two highest areas of perceived eagle risk (see Figure 5.4) were very close to two known nesting sites of breeding pairs of eagles; in the northwest a crowned eagle nest and in the east a black eagle pair (pers. obs.). All of these factors indicate a strong spatial variation in eagle risk throughout the landscape.

The most likely explanation for the differing responses to eagles from the two species is again due to samango monkeys' arboreal nature. A common response to an eagle alarm call was for many members of the group to retreat downwards (see also Cords 1987, Macleod 2000, Cordeiro 2003); this is likely to be a defensive response, indicating that lower height signifies reduced eagle predation threat. Therefore, the terrestrial nature of vervets (Gebo & Sargis 1994) perhaps suggests an overall reduced eagle predation risk, potentially explaining the lack of spatial response to perceived eagle risk found by Willems and Hill (2009b).

5.4.2 Leopard predation risk

Although Papworth et al. (2008) detected a leopard-specific alarm vocalisation, the adult males' "pyow" call, from a population of samango monkeys in Uganda, I recorded no evidence of such a call. The "pyow" call was often used by the alpha male; however, there was no evidence it served a function as an alarm call. Previous studies have attributed the male "pyow" call as a territory call (Marler 1973, Cords 1987) and this may be the function at Lajuma. Papworth et al. (2008) have been the only study to describe a leopard-specific samango alarm call, although Brown (1989) previously identified the "pyow" call as having the general characteristics of an alarm call. Therefore, it appears the "pyow" call is serving

different functions in different samango populations, an occurrence which merits further research in other geographically distinct samango populations.

The lack of a leopard-specific alarm call at Lajuma at first suggests low predation risk from leopards. Lajuma has a high density of leopards (Chase-Grey 2011), but factors such as habitat structure or the presence of preferred food sources might mean a relatively low leopard predation risk for the samangos. This is further confirmed by samangos making up a small proportion of leopard diet in the area (2.1%, Chase-Grey 2011). However, previous studies have shown samangos to consider the understory a high risk area of predation (Emerson et al. 2011, Gaynor & Cords 2012). There is no evidence that other potential terrestrial predators, such as baboons or snakes contribute to this high perceived terrestrial predation risk. The samangos on site, therefore, may simply be good at avoiding leopard predation and leopard predation may not be a strong enough selective pressure to drive the evolution of a leopard-specific alarm call.

The evolution of a leopard-specific alarm call at the study site is surprising given the relatively low density of leopards in the Budongo Forest, Uganda (Newton-Fisher, N.E., pers. comm.). However, although the leopard density in Budongo is currently low, it may have been much higher previously which might explain the enduring leopard-specific alarm call. This similarly may be the case for Lajuma; the lack of a leopard-specific alarm call might be due to Lajuma, until recently, having a low density of leopards.

Another option, for the results of Papworth et al. (2008) is that the Budongo alarm call is not leopard-specific but terrestrial predator-specific and has evolved over time due to a high predation risk from other terrestrial predators on site, such as chimpanzees. Other possibilities are that a leopard-specific alarm call is used rarely by the Lajuma samangos and so was simply not observed during the study period, or that the call was indiscernible from observed calls and was therefore recorded by the observer as an unknown alarm call.

5.4.3 Baboons

Willems and Hill (2009b) showed that the risk of baboon predation was a very strong determinant of vervet space use. However, the samango monkeys did not appear to treat the baboons as a predation threat; indeed they often fed side by side in the same tree (pers. obs.). Communication with experts revealed that they are not aware of any sites where baboons feed on samango monkeys, so this lack of predation from baboons is not unusual (Cords, M. and Lawes, M.J., pers. comm.). There are a number of possible explanations for this: firstly samango monkeys are slightly larger than vervets (Harvey et al. 1987, Bolter & Zihlman 2003) which perhaps increases the risk of injury to baboons, increasing the cost of attempted predation for the baboons. Secondly, being more arboreal, the samangos are likely to be more agile in the trees than vervets and therefore more difficult to catch. A third possibility is a consequence of samango feeding behaviour. The samangos often took only one bite of a fruit and then dropped it to the ground, especially when feeding on larger fruit. This behaviour is often considered a seed dispersal technique (Howe 1980, Kaplin & Moermond 1998, Lambert 1999) and may provide baboons and other terrestrial animals with fruit from the ends of branches to which they would otherwise have no access. This type of association has been observed previously at Lajuma (Seufert et al. 2010) and has also been documented amongst samangos and baboons in Uganda (Struhsaker 1981). The energy gain to baboons from such an association may outweigh any energy gain from directly feeding on samangos. A final possible explanation is that the baboons at Lajuma simply do not consider samango monkeys as a possible food source.

5.4.4 Inter-group encounters

There are a number of possible explanations for the lack of an effect of inter-group encounters on space use. First, samangos are able to recognise the presence of another group in their territory at a large distance. The group would often move quickly many hundreds of metres towards the competitor group before an inter-group encounter occurred. Thus, it is possible that the samangos do not need to patrol these areas as long as they are prepared to move quickly once they recognise a threat from a distance. Samangos have a variety of different

vocalisations, such as the male's boom call, which can be heard up to 1km away (Brown 1989), suggesting that auditory monitoring of the home range boundary should be relatively easy for a group. Second, the rareness of physical contact between the two groups during encounters, suggests that competitor groups may not be a high injury risk and so the focal group may not actively avoid areas of high inter-group encounter risk. A previous study (Lawes & Henzi 1995) into samango monkey inter-group encounters concluded that 48% of inter-group encounters were food related; but could not come to a satisfactory conclusion to explain the remaining 52%, suggesting that territory defence and mate defence may be partly involved. This lack of conclusion from the Lawes & Henzi (1995) study suggests the potential effects of inter-group encounter risk on ranging may be highly complex; which may go some way to explaining why no overall effect was observed in this study.

5.4.5 Habitat usage

Considering that samangos are arboreal specialists it was not surprising that tall forest was the most preferred habitat type and that the monkeys were significantly avoiding areas of lower canopy height. When evaluating purely on the basis of canopy height the only surprise is the significant avoidance of riverine forest which is the habitat type with the highest average canopy height. However, the majority of riverine forest is found along the eastern edge of the home range, well away from the core area. The vervet monkeys in the Willems & Hill (2009b) study group had no habitat types that they significantly avoided. This is perhaps best explained by the difference in the evolutionary niche each species occupies. The arboreal adapted samango monkeys would be expected to spend little time in areas of low vegetation density and/or of low average canopy height; whereas, the more generalist, semi-terrestrial vervets would be expected range more in a variety of habitats.

5.4.6 Food availability

An unexpected result was the lack of a significant relationship between space use and fruit availability. There is, however, a strong positive relationship between fruit availability and canopy height. The strong positive relationship between canopy height and range use may partially explain the lack of effect of fruit availability observed. This is supported by the samangos' preference for areas of tall forest and their significant avoidance of other habitat types, with the exception of short forest. When ranked in order of fruit availability (Table 4.4) the results show that the samangos avoided areas with a high food density. However, when ranked in order of canopy height, tall forest and short forest constitute two of the top three tallest habitat types. Food availability also has a strong negative relationship with understory visibility. However, the monkeys strongly prefer areas of high visibility, so the lack of food availability effect might be explained by the strength of the preference of high visibility/avoidance of low visibility areas.

Another possible explanation for the absence of a relationship between utilisation and food availability is the lack of competition from other species for food. The vervets at Lajuma were extremely low in number at the time of the study, and there are few other species which rival the samangos for their food sources. Therefore, an abundance of food may have existed within the home range. The samango population on site has been steadily increasing in number for several years (Gaigher, I. G., pers. comm.), suggesting that food may not have been a strong limiting resource for the monkeys during my study. If this is the case then the monkeys may able to base their movement decisions on other factors such as reducing predation risk.

Another potential reason for the lack of effect of food availability involves the use of cheek pouches. Cheek pouches are a conserved morphological trait in all Cercopithecines (Murray 1975) and are thought to have an anti-predation function, allowing a monkey to spend time consuming food in lower risk areas than where the food is located (Smith et al. 2008). The use of cheek pouches is a well-documented behaviour in samango monkeys (Rowell & Mitchell 1991, Kaplin et al. 1998, Smith et al. 2008) and could theoretically contribute to the lack of an

effect of food availability on ranging. This would be the case if the monkeys spent a small amount of time in areas of high food availability, filling their cheek pouches, and then moved to areas of low food availability, but increased safety from predators, to consume the stored food.

Finally, there is a problem with using annual fruit availability in a spatial context because fruit availability varies seasonally (Figure 3.2). Therefore, some areas may have high fruit availability for a few months, but the rest of the year have very little. This may contribute to the lack of effect from food availability seen in the analyses, as any seasonal movements to areas of high fruit availability may be diluted by the use of an annual figure.

5.4.7 Canopy height

As an arboreal species it was expected that canopy height would have a strong effect on the ranging behaviour of the group and the analyses from this study showed this was the case, with samangos preferring areas of taller canopy. There are a number of possible reasons for the observed effect of canopy height on samango monkey ranging behaviour, for example being higher in trees decreases predation risk from terrestrial predators (Struhsaker 1967b, Hart et al. 1996). According to a previous study the samangos at Lajuma perceive less risk when higher in trees (Emerson et al. 2011) which may explain the observed preference for ranging in areas of taller canopy.

5.4.8 Visibility

The analyses suggest that samangos prefer areas of high understory visibility. The overall effect of perceived eagle predation risk suggests that the samangos alter their behaviour to reduce their risk of predation. By using higher visibility areas they might be increasing their ability to detect predators whilst also reducing the ability of predators to conceal themselves. The samangos at Lajuma prefer clear sight lines (Emerson et al. 2011) and this could be a major contributing factor towards the preference for high visibility areas. In a previous study, vervet

monkeys were observed moving into an otherwise previously unused area after it was affected by a forest fire, and this was attributed to decreased predation risk due to increased visibility (Jaffe & Isbell 2009). Hill & Weingrill (2007) observed that chacma baboons preferred areas of high visibility due to the associated decreased level of leopard predation risk. Finally, vervet monkeys have also been observed to reduce vigilance when in areas of higher visibility, indicating a reduction in predation (Chapman 1985, Enstam & Isbell 2002). These studies suggest that the preference samangos show for high visibility areas is likely an aspect of predation avoidance.

It must be considered that the visibility measurements used in this study were taken at a height of 2m. The monkeys spend the majority (60.3%) of their time above 2m (data from adult scan samples). The visibility higher in the canopy may be different to the recordings made nearer the ground. However, these recordings may still give us good information on the possible effect on behaviour from terrestrial predation risk. The monkeys may be using areas of high understory visibility in order to increase their ability to remain vigilant for such predators.

5.4.9 Conclusions

This study is the first to use detailed data on perceived predation risk, inter-group encounter risk and environmental variables, such as food availability and visibility, to investigate range use in an arboreal monkey species. The results showed perceived eagle predation risk exceed the effects of resource distribution. This suggests that spatially varying predation risk should always be considered a potentially important factor when studying range use in a primate species. The results from this study differed from those for vervet monkeys (Willems & Hill (2009b) which showed no effect of perceived eagle risk on ranging, but significant effects on ranging from perceived risk of terrestrial predators. The different effects of predation risk observed between samangos and vervets are most likely explained by their preferences for arboreal or semi-terrestrial lifestyles. A primate spending more time on the ground is more likely to suffer a higher predation risk from terrestrial predators such as leopards and vice-versa for more arboreal

species (Isbell 1994). However, the two species may experience different overall levels of predation risk. A total of 385 alarm calls were recorded for the vervets in 84 days; whereas just 131 alarm calls were recorded for samangos in 96 days. These differences may suggest the vervets are under a higher overall predation pressure than the samangos. Such differences have been suggested as a common pattern between terrestrial and arboreal primate species (Terborgh & Janson 1986) and also between multi-male, multi-female and single-male, multi female primate groups (van Schaik & Horstermann 1994). These potential differences provide an interesting possible avenue for future research investigating the factors affecting predation risk in two species sharing similar geographical areas.

The next step in this study is to investigate the factors which effect vigilance behaviour. This will be achieved via two different investigations. The first is an investigation into behavioural effects, such as activity type, on vigilance (Chapter 6). The second investigates the factors which drive spatial variation in vigilance behaviour (Chapter 7), allowing comparison with the results presented in this chapter.

Chapter 6

Intra-Group Effects on Vigilance Behaviour

6.1 Introduction

Predation risk often varies over space and time (Lima 1998, Lima & Bednekoff 1999). One of the most common anti-predator behaviours is to remain visually vigilant for predators (Bednekoff & Lima 1998); however, most animals are unable to forage and remain vigilant at the same time (Underwood 1982, Lima 1998). This often leads to a trade-off occurring between time spent vigilant or time spent feeding (Brown 1999). To approach this trade-off as efficiently as possible, primates will base their decisions on the risk they perceive at that time. At high risk times this potentially means decreasing time spent feeding to increase vigilance time or halting feeding altogether to monitor their surroundings as extensively as possible (Heymann 1990). Therefore, some activities a primate engages in may be prohibitive of vigilance, which can lead to further important effects on their overall behavioural ecology, and eventually their fitness.

6.1.1 Activity

Activities vary by the level of visual attention they require. For example, it is difficult for primates to forage and remain visually vigilant simultaneously, because foraging requires them to search and handle food (Pulliam 1973, Treves 2000, Hill & Cowlishaw 2002). In contrast, there may be no other requirements of an individual's attention while resting so they might be able to spend a large proportion of their time vigilant, with sleeping being the obvious exception (Cowlishaw 1998). Many primate studies have observed such a pattern of increased vigilance when resting, but lower vigilance whilst feeding, for example

in ursine colobus monkeys (Teichroeb & Sicotte 2012), chacma baboons (Cowlishaw 1998), brown capuchin monkeys (van Schaik & van Noordwijk 1989, Hirsch 2002), white-fronted capuchins (*Cebus albifrons*) (van Schaik & van Noordwijk 1989) and moustached tamarins (Stojan-Dolar & Heymann 2010a).

Allogrooming may have varied effects on vigilance behaviour. Grooming another individual generally requires the majority of the groomer's attention (Maestripieri 1993), so vigilance is likely to be low (Maestripieri 1993, Stojan-Dolar & Heymann 2010a). Conversely, whilst being groomed there should be no other demands on an individual's attention, so vigilance may increase, perhaps on a par with time spent vigilant whilst resting. However, the only primate evidence seems to point to the contrary, with a number of studies observing a decrease in time vigilant whilst being groomed (Cords 1995, Stojan-Dolar & Heymann 2010a). These results suggest that the individuals involved chose to groom at times when risk is considered low (Cowlishaw 1997), although Cords (1995) observed no evidence that samango grooming occurs in safer locations or at safer times of day.

So far vigilance has only been discussed in terms of the ability of an individual to remain vigilant during certain activities. The foraging/vigilance trade-off suggests that when an individual is foraging, its risk of predation might be higher because vigilance is reduced. However, this suggestion does not take into account that most primate species live in groups, which can reduce the overall level of predation risk for a number of reasons (van Schaik 1983).

6.1.2 Group living

Group living in primates has been shown to be a fundamental aspect a group's anti-predation strategy (Alexander 1974, van Schaik 1983). The larger a group is the safer an individual is from predation (van Schaik 1983, Dunbar 1988), because group living reduces predation risk for individuals for three main reasons: the "dilution effect", where increased numbers of prey reduces the overall risk of each individual being preyed upon (Hamilton 1971, Dehn 1990), predator deterrence (Maisels et al. 1993) or the "detection effect", where an increase in the number of

potentially vigilant individuals increases the chances of identifying a predation threat (Cresswell 1994).

A reduction in predation risk due to group living means an individual may be able to reduce their time spent vigilant, allowing them more time to forage. Many groups even coordinate their vigilance, which further improves their ability to efficiently trade-off foraging and vigilance (Sirot & Touzalin 2009). An excellent example of this cooperative strategy is meerkats (*Suricata suricatta*), where individuals act as sentinels, allowing one or a few individuals to fulfil the vigilance responsibilities for the entire group (Clutton-Brock et al. 1999).

Concordant with the anti-predation hypothesis several primate studies have observed vigilance decreasing with increasing group density (van Schaik & van Noordwijk 1989, Rose & Fedigan 1995, Cowlishaw 1998, Treves 1998, Steenbeek et al. 1999, Treves et al. 2001, Smith et al. 2004, Stojan-Dolar & Heymann 2010a, Teichroeb & Sicotte 2012). This pattern is not ubiquitous in the primate literature, however, as vigilance is often aimed towards other members of the group (Caine & Marra 1988), so increasing group density may cause vigilance to increase (Treves 1998, Hirsch 2002, Kutsukake 2007). Such social monitoring may reduce time available for predator vigilance and thus increase the risk of predation (Treves 2000). Vigilance strategies depend on whether individuals consider predators or conspecifics bigger threats. In chimpanzees, where infanticide is a high risk, it appears that vigilance is mostly aimed at conspecifics (Kutsukake 2006, 2007). In contrast, tamarins, which adopt a communal care strategy in which non-family members often care for infants, consider predators a more important threat (Smith et al. 2004, Stojan-Dolar & Heymann 2010a). Therefore, when investigating the vigilance behaviour of a species it is important to consider their intra-group ecology before attempting to make judgements.

6.1.3 Height

The majority of primates are at least semi-arboreal (Fleagle 1999), spending much of their time in trees. Some may consider the risk from terrestrial predators such

as big cats to be important and therefore may associate the lower canopy with a higher risk (Steenbeek et al. 1999); others may consider risk from arboreal predators such as raptors to be more important and may associate the upper canopy with a higher risk (Baldellou & Henzi 1992). These preferences would be likely to show in their vigilance behaviour. Thomas' langurs increase their vigilance when lower in the canopy, which was attributed to the increased predation risk associated with that height from terrestrial predators (Steenbeek et al. 1999). Similarly, moustached and saddleback tamarins (Smith et al. 2004) and brown capuchin monkeys have been observed to increase vigilance nearer the ground. Conversely, vervet monkeys increase vigilance when at the very top of the canopy due to the potential risk from raptors (Baldellou & Henzi 1992).

6.1.4 Time

Predation risk may vary temporally both on short and long term scales, which may have important effects on how prey animals vary their anti-predator strategies over time. Predation risk may vary through the day (Lima & Bednekoff 1999) and one of the biggest potential sources of this variation lies in predator hunting preferences. For example, African black eagles in the Northern Cape, South Africa, have been shown to prefer to hunt in the middle of the day, where the use of thermals aids their ability to hunt rock hyraxes (Druce et al. 2006). Whereas, leopards utilise stealth hunting and so prefer to hunt in lower light levels (Bailey 1993). Prey animals may therefore choose to forage at times when risk is lower due to lower predator hunting preference. This would also likely mean an increase in vigilance at times of higher preference. Predation risk may also vary seasonally (Lima & Bednekoff 1999). An example of this effect has been observed in mongoose lemurs and brown lemurs which shift from diurnal to more crepuscular activity cycles during the dry season, when the lower vegetative cover increases risk of predation by raptors (Rasmussen 2005). During the daylight hours there would likely be a reduction in time spent foraging, which would potentially allow increased time vigilant, leading to a reduction in predation risk.

6.1.5 Glance rates

Time spent vigilant does not fully capture an animal's vigilance behaviour. A potentially important element of vigilance behaviour is glance rate, defined as the number of attention shifts per unit time. By maintaining a high glance rate an individual may still be able to monitor its environment, maintaining a sufficient level of vigilance, whilst engaged in other activities which require its attention (Gluck 1987, Cowlishaw et al. 2004). Although many primate studies have investigated variation in time spent vigilant, few have investigated the causes of glance rate variation. For example, Alberts (1994) observed that juvenile female yellow baboons glance significantly more frequently than their male counterparts. Rhesus macaque (*Macaca mulatta*) mothers significantly decrease their infant directed glance rates whilst allogrooming (Maestripieri 1993) while captive black tufted-ear marmosets (*Callithrix penicillata*) have significantly higher aerial than terrestrial glance frequencies (Nunes et al. 2010). These studies suggest that glance rates may be an important element of primate vigilance behaviour. However, due to a lack of previous research little is known about the causes of glance rate variation. The foraging/vigilance trade-off may force an individual to balance their time between foraging and vigilance, but by increasing glance rate an individual may still be able to adequately monitor its surroundings whilst allocating adequate time to foraging.

6.1.6 Samango monkeys

Samango monkeys live in groups with up to 65 individuals (Butynski 1990, Beeson et al. 1996, Smith et al. 2004, Houle et al. 2010, Lawes et al. 2011). They face threats from several predators, including leopards (Hayward et al. 2006), eagles (Skorupa 1989, Struhsaker & Leakey 1990), snakes (Foerster 2008) and chimpanzees (Wrangham et al. 1990, Mitani & Watts 1999). Due to these threats they have evolved a complex alarm call system which is predator-specific towards raptors (Brown 1989) and, at one site in Uganda, towards leopards (Papworth et al. 2008). These characteristics suggest that samangos may also employ complex vigilance strategies.

In relation to the effect of activity, one previous samango study observed vigilance to decrease whilst feeding when compared to resting (Cowlishaw et al. 2004), a result similar to other non-samango studies which have already been mentioned. The results of these studies suggest that this will be a likely pattern in the Lajuma samangos. With regard to the effect of nearby conspecifics, Treves (1999) observed that samangos in Kibale Forest, Uganda decreased vigilance when other group members were in close proximity, whilst Cords (1990) observed that samango monkeys in Kakamega Forest, Kenya, decrease time spent looking upwards for aerial predators when in mixed species association with red-tail monkeys. Samangos generally show low intra-group aggression (Cords 2002a; pers. obs.) and so most samango vigilance is likely to be aimed at predators rather than conspecifics. Therefore, due to factors such as the "detection effect" the presence of nearby conspecifics is likely to decrease the risk to an individual, allowing for a reduction in overall time spent vigilant.

Using a giving-up density experimental procedure on the same population as this study, Emerson et al. (2011) showed that the samangos leave higher densities of food at ground level than higher up. These results indicate that the samangos consider lower heights a higher risk of predation, a finding consistent with the results of another samango study in Kenya, which observed vigilance to increase nearer the ground (Gaynor & Cords 2012). However, results have shown the focal group perceive eagles to be a higher predation risk than terrestrial predators (Section 5.3), which would predict an increase in vigilance higher in the canopy. Therefore, there may be two peaks of predation risk for the samangos: one nearest the ground where risk from terrestrial predators is likely to be high and the other higher in the canopy where risk from eagles is likely to be high.

A characteristic unique to Cercopithecine monkeys, such as samangos, is the presence of cheek pouches (Lambert 2005). Cheek pouches may reduce potential feeding competition and reduce predation risk through allowing individuals to collect food in their pouches and then move to a safer area for further processing (Smith et al. 2008). There are two possibilities regarding vigilance and the usage of cheek pouches: vigilance may increase whilst feeding from cheek pouches, as

the activity requires no alternative usage of the animal's attention; alternatively, vigilance may decrease because of the potential for the animal to move to a location it considers lower risk.

6.1.7 Objectives

The aim of this study is to investigate the factors that influence the proportion of time vigilant and glance rate in samangos. No previous study has attempted to explain in such detail the variation in both of these elements of vigilance behaviour of primate species. The chapter will test the following predictions:

1. Time spent vigilant will be higher when resting; however, will be lower during periods of feeding and allogrooming.
2. Glance rate will be higher whilst feeding than while resting.
3. Time spent vigilant will decrease as the number of nearby individuals increases.
4. Vigilance will be highest both at the top of the canopy and when on the ground.

6.2 Methods

6.2.1 Study site

The study was based at the Lajuma Research Centre, a 4.3km^2 area located in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). The altitude of the study site is approximately 1300m and local climate is described as temperate/mesothermal, with cool dry winters from April-September and warm to hot wet summers from October-March (Willems 2007). Potential samango predators at Lajuma are the leopard, crowned eagle, African black eagle and the African rock python. Furthermore, there are a number of venomous snakes present which do not actively prey on samangos but still pose significant mortality threats and therefore may affect vigilance behaviour. For a comprehensive description of the study site see Section 2.2.

6.2.2 Study species

Samango monkeys are primarily frugivorous (Lawes 1991), medium sized, arboreal guenons. Samangos have a variety of vocalisations, with a number classed as alarm vocalisations. These include an alarm call which has been well documented as referentially specific to aerial threats such as raptors (Brown 1989, Papworth et al. 2008).

6.2.3 Data collection

A habituated samango group of approximately 40 individuals was observed over a 16 months period (Oct 2009-Dec 2010), with vigilance data collected in the last 11 months. The same resident male was present throughout this period and no other adult males were observed within the group for significant periods of time. Adult females numbered 10-12 individuals during the study. Behavioural data collection consisted of eight successful follow days per month (totalling 96 days). Data were collected on a palmtop (Sony Clie SL-10) with behavioural data collection software (Elan 2.0.1 and Pendragon Forms 4.0).

Vigilance was defined as a visual search of the environment beyond the immediate vicinity (Treves 2000). Vigilance type was separated into eight categories (Table 6.1). A separate category was used to indicate moving, due to the difficulty in recording accurate vigilance data when the focal individual was not stationary. These time periods were then excluded from analysis. Vigilance data were recorded using 5 minute continuous focal samples, with a maximum of 2 minutes "out of sight". Each time a change in vigilance category occurred a recording of the time of the change was noted.

Eight adults (seven females and the alpha male) were individually identified for focal sampling. Each day was split into four quarters of equal length, and each individual was sampled once in each quarter per month. Five adults (including the male) were sampled for the entire 11 months, two females were sampled for 10 full months with one and three samples completed in December. One final female was sampled for eight full months (Table 6.2).

At the beginning of each sample period behavioural data were recorded on individual I.D., time, activity type, height of focal individual and number of individuals within 5m. The activity types used were: resting, feeding, eating from pouches, grooming, being groomed and other socialising. During the sample each change in activity type was immediately noted along with the time. Once a minute a note was made of any changes in the remaining behavioural categories as it would have been too difficult to record changes in these instantaneously whilst also continuously monitoring vigilance behaviour.

Table 6.1 Descriptions of vigilance categories used in data collection.

Vigilance type	Description
Social	Looking towards group members or at a specific individual
Look-up	Looking towards the sky for an aerial threat
Look-down	Looking towards the ground for a terrestrial threat
Scanning	Scanning horizontally
Observer	Looking directly at the observer
No Vigilance	Not being vigilant
Out of sight	Face obscured
Moving	Individual was moving

Table 6.2 Number of continuous samples completed throughout the study period.

Period	Feb-Sept	Oct	Nov	Dec	Total
No. of samples	32 (per month)	28	28	24	336

6.2.4 Statistical analysis

The vigilance data set violates all three of the most important assumptions of parametric tests. First, the proportion of time vigilant is not normally distributed (Figure 6.1; Kolmogorov-Smirnov Test, N=761, Z=3.093, p=<.001). A number of transformations were attempted but normality could not be achieved. Second, sample sizes within all the categories were not homogeneous. For example, there were 350 samples whilst the focal individual was feeding, but only 35 whilst grooming another individual. Third, variance within all categories was high (Levene's Test, F=1.971, p=<.001). With such data it was highly unlikely that a traditional statistical test would produce robust results. Therefore, a customised model which was not constrained by the assumptions of such tests was built.

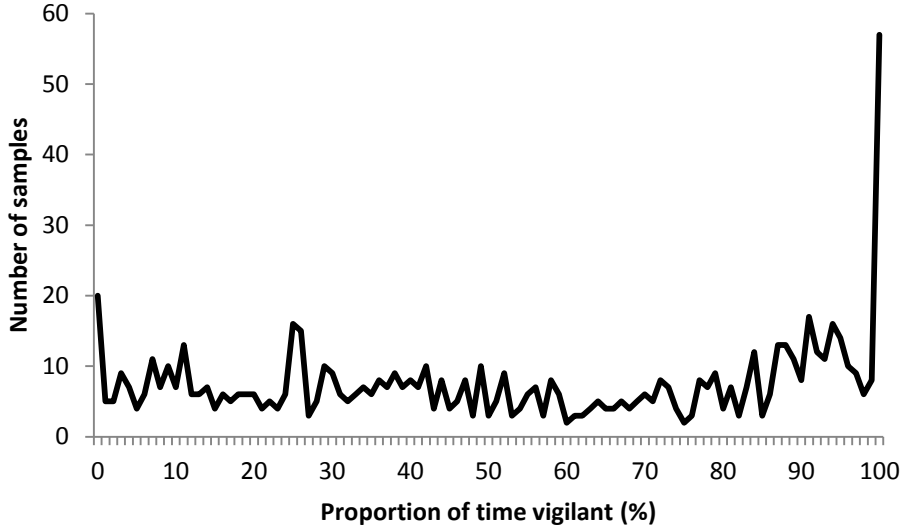

Figure 6.1 Distribution of samples (≥30 secs) within all categories and converted to proportion of time.

The constructed model utilised a likelihood function quantifying the probability that the hypothesis matched the observed data (Richards et al. 2011). Such a model allows for the introduction of multiple discrete or continuous variables without the normality constraints associated with traditional models (Pawitan 2001). For a detailed overview of the likelihood approach, see Pawitan (2001). Due to the complexity required to form a model able to analyse the effects on all

vigilance categories, only a dependent variable representing overall vigilance could be used. Data in the categories "unknown" and "moving" were excluded from the dataset and the sample duration was recalculated. Next the vigilance categories "scanning", "look-up", "look-down", "social" and "observer" were combined, leaving two variables: glance periods, either time vigilant or non-vigilant. In this instance, a glance period represents the time between each attention shift, either from vigilant to non-vigilant, or vice-versa. By understanding the mean vigilant and non-vigilant glance periods it is possible to calculate both a proportion of time vigilant and a glance rate. Glance rate was defined as the number of attention shifts per minute.

The results were filtered so that each glance period was displayed alongside the behavioural conditions at that time. The independent variables used as behavioural conditions can be seen in Table 6.3. This yielded a total sample size of 3496 vigilance periods and 3651 non-vigilance periods. The modelling framework determined expected glance rates based on sample means and calculated the likelihood of the observed glance rate in that situation. To achieve this, predicted glance rates were calculated using the following equation:

$$\mu_{ij}(x_1, x_2, x_3, x_4) = \beta_0 \exp\left(\beta_i + \beta_j + \sum_{k=1}^{4} \beta_k \left(\frac{x_k - \bar{x}_k}{\delta_k}\right)\right)$$

Where μ is the expected glance period, β represents a dimensionless variable indicating an effect on mean glance period, β_0 is the mean glance period if all sample sizes were equal, i represents a focal individual, j represents an activity type, k represents one of four scale categories (Table 6.3), with x indicating the observed measurement, $\bar{x}$ the mean of all measurements and δ the standard deviation (Table 6.4).

Table 6.3 Independent variables included in the models.

Variable	Description
Individual	Identity of focal individual
Activity Type	Resting, feeding, eating from pouches, grooming, being groomed (see Section 2.4.6 for definitions)
Height	Height of focal individual off ground (in metres)
Neighbours	Number of juveniles and adults within 5 metres
Temperature	Mean monthly temperature of the month the sample was taken
Time	The hour of the day the sample was taken

Table 6.4 Means ($\bar{x}$) and standard deviations (δ) for scalar categories used in the models. See Table 6.3 for definitions of the variables.

No.	Variable	Vigilance		Non-vigilance	
		$\bar{x}$	δ	$\bar{x}$	δ
1	Neighbours	1.77	1.88	1.80	1.89
2	Height	2.89	2.18	2.88	2.19
3	Temperature	19.07	4.16	19.08	4.17
4	Hour	11.45	3.03	11.45	3.04

The equation assumes the relationships between glance period and the independent variables are linear. The log-likelihood of the model assumed that the variation in the observations about the predicted mean had a negative binomial distribution; the plotted distributions of the glance periods were consistent with this assumption (Figure 6.2). Parameters were estimated by maximising the log-likelihood, which was achieved using the Microsoft Excel (2010 Version, Microsoft, Redmond, Washington) optimisation routine add-on "Solver".

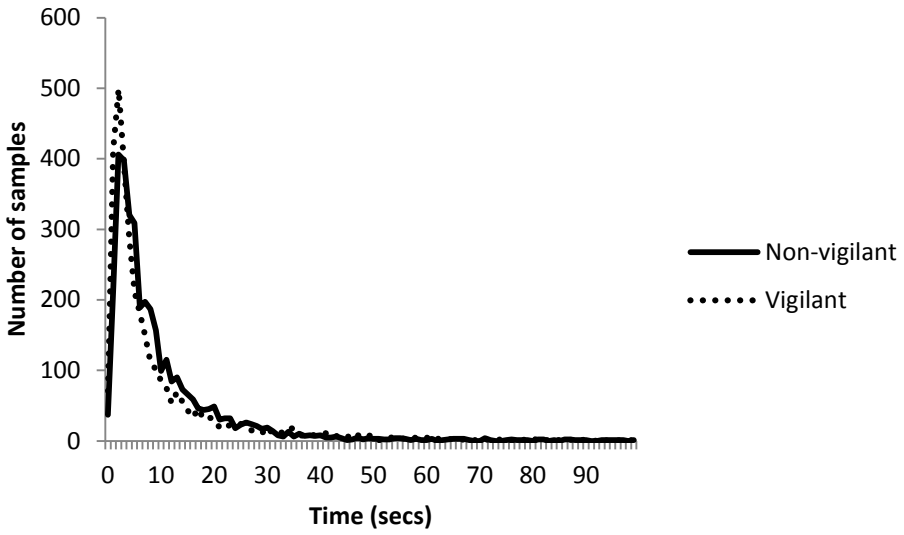

Figure 6.2 Distribution of vigilant and non-vigilant glance periods within all samples.

Individual and activity type were included in all models due to their likely biological significance. The remaining four categories were included in the models in all possible combinations (totalling 16 models). Models were selected using AIC, based on the two-step procedure suggested by Richards (2008).

To confirm the results from the model and to further understand the possible effects of interactions between activity type and the other covariates, the data were split into two different datasets: feeding and resting. Eating from pouches was considered a sub-category of resting and was included in the resting dataset. Separate likelihood models were run using these two datasets. For means and standard deviations for scale categories for the feeding-specific models see Table 6.5 and for the resting-specific model see Table 6.6.

Table 6.5 Means ($\bar{x}$) and standard deviations (δ) for scalar categories used in the feeding-specific models. See Table 6.3 for definitions of the variables.

	Vigilance		Non-vigilance	
Variable	$\bar{x}$	**δ**	$\bar{x}$	**δ**
Height	2.76	2.27	2.78	2.27
Hour of day	11.57	3.18	11.56	3.19
Neighbours	1.70	1.82	1.69	1.81
Temperature	18.41	4.13	20.61	3.77

Table 6.6 Means ($\bar{x}$) and standard deviations (δ) for scalar categories used in the resting-specific models. See Table 6.3 for definitions of the variables.

	Vigilance		Non-vigilance	
Variable	$\bar{x}$	**δ**	$\bar{x}$	**δ**
Height	3.10	2.04	3.10	2.06
Hour of day	11.31	2.83	11.29	2.84
Neighbours	1.74	1.89	1.74	1.89
Temperature	20.61	3.76	20.61	3.77

6.3 Results

6.3.1 Main model

16 models were assessed for selection and four met the selection criteria (Table 6.7). These were Models 4 and 7 for the vigilance dataset, and Models 1 and 4 for the non-vigilance dataset. The two simplest models (least number of independent variables) within a ΔAIC score of 6 were selected for description and interpretation. For vigilance data this was Model 7, which included the independent variables activity type, focal individual, height of focal individual, number of nearby individuals. For non-vigilance data this was Model 4, which included the same variables as the vigilance model, plus mean monthly temperature. From the four models which fitted the AIC selection criteria, hour of day was absent as a variable in three of them. This indicates the hour of day has a very little effect on the vigilance behaviour of the samangos. Similarly, mean monthly temperature was not present in all selected models.

Table 6.8 displays the effects of the included factors from the two selected models. Although the effects displayed in the table are dimensionless they show a relative effect of the independent variables on glance period. A positive score indicates that factor causes an increase in glance period compared to the mean, whereas a negative score indicates a decrease. The larger the score the larger the effect.

Table 6.7 Number of factors included in each model (K) plus maximum log likelihood (LL) and ΔAIC's. Also displayed are predictors included in each model: H (height of focal individual), Ho (hour of day), I (number of individuals within 5 metres) and T (mean monthly temperature). Individual and activity type were included as variables in all models. Models with ΔAIC ≤6 and lower than all simpler versions are highlighted in bold. Sample size for vigilance models =3496 and for non-vigilance models = 3651.

Model			Vigilance		Non-vigilance	
No.	**Predictors**	**K**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
1	H, Ho, I, T	18	-11565.9	1.8	**-12166.5**	**0.0**
2	H, Ho, I	17	-11569.3	6.7	-12175.2	15.5
3	H, Ho, T	17	-11577.5	23.0	-12173.1	11.3
4	H, I, T	17	**-11566**	**0.0**	**-12167.5**	**0.02**
5	Ho, I, T	17	-11622.2	112.4	-12195.9	56.9
6	H, Ho	16	-11582.5	31.1	-12180.6	24.3
7	H, I	16	**-11569.4**	**4.8**	-12176.1	15.2
8	H, T	16	-11577.5	21.1	-12174.3	11.6
9	Ho, T	16	-11643.8	128.6	-12198.8	60.7
10	Ho, I	16	-11631.3	128.6	-12213	88.9
11	I, T	16	-11623.1	112.3	-12198.9	60.9
12	H	15	-11582.5	29.1	-12181.6	24.3
13	Ho	15	-11657.4	178.8	-12214.5	89.9
14	I	15	-11631.9	127.8	-12216	93.0
15	T	15	-11644.6	153.1	-12201.9	64.8
16	None	14	-11657.7	177.5	-12217.6	94.1

There appears to be differences between the focal individuals, indicating that it was judicious to include their effects in every model. The male has slightly shorter than average vigilance glance periods, but much longer than average non-vigilant glance periods, indicating a lower than average proportion of time spent vigilant than compared to the other focal individuals. The male's long non-vigilant glance

periods also likely mean a longer than average glance rate. With much shorter than average non-vigilant glance periods it appears that female 3 spent the highest proportion of time vigilant. This result also means that female 3 has a relatively short average glance rate.

Resting and eating from pouches have a positive effect on vigilant glance periods and a negative effect on non-vigilance glance periods indicating a higher than average proportion of time spent vigilant during these activities. However, the opposite effects from these activities on the different periods mostly cancel each other out in terms of the potential effects on glance rate. The negative effect on both vigilant and non-vigilant glance periods indicates a lower than average time spent vigilant and glance rate when feeding. The opposite effect can be seen when being groomed, with positive effects on both vigilant and non-vigilant glance periods, indicating a lower than average time spent vigilant and glance rate. Finally the very strong positive effect of grooming on non-vigilant glance periods indicates a much lower than average time spent vigilant and glance rate during this activity.

The more nearby individuals leads to longer non-vigilant glance periods and shorter vigilant glance periods. This means that as number of nearby individuals increase so does time spent vigilant. The opposing effects on the two glance periods likely cancel each other out in regard to glance rate, meaning that nearby individuals likely have little effect on glance rates. Increasing height has a positive effect on both vigilant and non-vigilant glance periods, although the effect on the vigilant periods is slightly stronger. This indicates that as height increases time spent vigilant will also increase and the positive effects on both types of glance period also indicate that as height increases glance rate will decrease. The difference between the two effects of .16 for nearby individuals and .09 for height indicates that the effect of 1 extra/less nearby individual on proportion of time spent vigilant may be slightly stronger than the effect of changing of height by 1m.

Table 6.8 Results of the two models selected for description and interpretation. β represents dimensionless variables indicating an effect on mean glance period, a positive effect indicates that factor causes an increase in glance period compared to the mean, whereas a negative score indicates a decrease. β_0 is the mean glance period if all sample sizes were equal. Independent variables are: focal individual (Individual), activity type (Activity), number of nearby individuals (Neighbours), height of focal individual (Height), hour of day (Hour), mean monthly temperature (Temperature).

		Vigilance Effects	**Non-Vigilance Effects**
Model Number		7	4
β_0		14.186	13.949
Individual		β_i	β_i
♀ 1		.098	-.040
♀ 2		.075	-.009
♀ 3		-.006	-.284
♀ 4		-.080	-.135
♀ 5		.013	-.077
♀ 6		-.010	.105
♀ 7		-.065	.134
♂ 1		-.026	.306
Activity		β_j	β_j
Resting		.362	-.586
Feeding		-.823	-.184
Eating from pouches		.562	-.847
Being groomed		.214	.340
Grooming		-.315	1.523
Other			
β_1	Neighbours	-.097	.063
β_2	Height	.224	.134
β_3	Temperature	ABSENT	.068
β_4	Hour	ABSENT	ABSENT

By working backwards through the model equation using the effect scores presented in Table 6.6 it is possible to convert the currently dimensionless effects into increases or decreases of seconds to the mean. This allows the calculation of mean proportion of time vigilant and glance rates for each variable, e.g. in different activities or at different heights.

6.3.2 Feeding- and resting-specific models

For the feeding-specific analysis the models which matched the selection criteria were 1 and 4 for the vigilance dataset and 1 and 3 for the non-vigilance dataset (Table 6.9). For the resting-specific analysis the models which matched the selection criteria were 1, 3 and 6 for the vigilance dataset and 1, 4 and 7 for the non-vigilance dataset (Table 6.10). Feeding-specific models selected for description and interpretation were Models 4 for the vigilance dataset and 3 for the non-vigilance dataset. Resting-specific models selected for description and interpretation were Models 6 for the vigilance dataset and 7 for the non-vigilance dataset.

For the feeding-specific model there were positive effects on time vigilant of height of focal individual and mean temperature (Table 6.11). The resting-specific model also indicated a positive effect of height of focal individual (Table 6.12). The effect size of height of focal individual in both models was similar, indicating no interaction between this and activity type on vigilance behaviour. Nearby individuals was excluded from two out of four of the selected models, thus the effects of nearby individuals were not selected for plotting. Being excluded from these models suggests there is no important interaction between the effects of nearby individuals and activity types on vigilance behaviour.

Table 6.9 Number of factors included in each feeding-specific model (K) plus maximum log likelihood (LL) and ΔAIC's. Also displayed are predictors included in each model: H (height), Ho (hour of day), I (number of individuals within 5 metres) and T (mean monthly temperature). Individual and activity type were included as variables in all models. Models with ΔAIC ≤6 and lower than all simpler versions are highlighted in bold. Sample size for vigilance models =2246 and for non-vigilance models =2317.

Model			Vigilance		Non-vigilance	
No.	**Predictors**	**K**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
1	H, Ho, I, T	14	**-6455.9**	**0.0**	**-7845.5**	**0.0**
2	H, Ho, I	13	-6471.1	28.5	-7851.9	10.9
3	H, Ho, T	13	-6468.8	23.8	**-7847.3**	**1.5**
4	H, I, T	13	**-6457.0**	**0.2**	-7850.6	8.1
5	Ho, I, T	13	-6493.8	73.9	-7862.0	30.9
6	H, Ho	12	-6488.4	61.0	-7853.1	11.2
7	H, I	12	-6473.3	30.8	-7857.4	19.9
8	H, T	12	-6470.4	25.0	-7852.5	10.0
9	Ho, T	12	-6516.7	117.2	-7862.4	29.9
10	Ho, I	12	-6516.5	117.2	-7873.7	52.4
11	I, T	12	-6493.9	72.0	-7870.5	46.0
12	H	11	-6491.5	65.2	-7858.7	20.4
13	Ho	11	-6548.3	178.8	-7873.7	50.5
14	I	11	-6517.1	116.3	-7883.8	70.6
15	T	11	-6516.9	116.1	-7871.0	45.1
16	None	10	-6549.7	179.6	-7883.8	68.7

Table 6.10 Number of factors included in each resting-specific model (K) plus maximum log likelihood (LL) and ΔAIC's. Also displayed are predictors included in each model: H (height), Ho (hour of day), I (number of individuals within 5 metres) and T (mean monthly temperature). Individual and activity type were included as variables in all models. Models with ΔAIC ≤6 and lower than all simpler versions are highlighted in bold. Sample size for vigilance models =1100 and for non-vigilance models =1167.

Model			Vigilance		Non-vigilance	
No.	**Predictors**	**K**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
1	H, Ho, I, T	14	**-4501.5**	**0.0**	**-3539.1**	**0.0**
2	H, Ho, I	13	-4504.0	3.0	-3540.8	1.4
3	H, Ho, T	13	**-4503.5**	**2.0**	-3547.9	15.7
4	H, I, T	13	-4505.7	6.3	**-3540.8**	**1.4**
5	Ho, I, T	13	-4525.7	46.5	-3552.3	24.5
6	H, Ho	12	**-4505.6**	**4.3**	-3549.2	16.1
7	H, I	12	-4508.3	9.5	**-3542.9**	**3.7**
8	H, T	12	-4507.8	8.5	-3549.3	16.3
9	Ho, T	12	-4529.7	46.2	-3557.1	31.9
10	Ho, I	12	-4526.6	46.2	-3556.1	30.0
11	I, T	12	-4530.0	53.0	-3553.0	23.9
12	H	11	-4509.9	10.8	-3550.9	17.5
13	Ho	11	-4530.2	51.3	-3560.1	35.9
14	I	11	-4530.9	52.9	-3557.2	30.2
15	T	11	-4534.1	59.1	-3557.7	31.2
16	None	10	-4534.6	58.2	-3561.1	36.1

Table 6.11 Feeding-specific model results selected for description and interpretation. β represents dimensionless variables indicating an effect on mean glance period, a positive effect indicates that factor causes an increase in glance period compared to the mean, whereas a negative score indicates a decrease. β_0 is the mean glance period if all sample sizes were equal.

		Vigilance Effects	**Non-Vigilance Effects**
Model Number		4	3
β_0		6.117	10.827
Individual		β_i	β_i
♀1		.227	.110
♀2		.112	.030
♀3		-.195	-.230
♀4		-.109	-.090
♀5		-.024	-.017
♀6		-.343	.084
♀7		-.030	-.065
♂1		.051	.179
Other			
β_1	Neighbours	-.120	ABSENT
β_2	Height	.200	.108
β_3	Hour	ABSENT	-.051
β_4	Temperature	.121	.065

Table 6.12 Resting-specific model results selected for description and interpretation. β represents dimensionless variables indicating an effect on mean glance period, a positive effect indicates that factor causes an increase in glance period compared to the mean, whereas a negative score indicates a decrease. β_0 is the mean glance period if all sample sizes were equal.

		Vigilance Effects	**Non-Vigilance Effects**
Model Number		6	7
β_0		22.029	7.115
Individual		β_i	β_i
♀1		.074	-.156
♀2		-.017	-.055
♀3		.137	-.386
♀4		.013	-.188
♀5		-.001	-.172
♀6		.205	.057
♀7		-.193	.398
♂1		-.218	.503
Other			
β_1	Neighbours	ABSENT	.123
β_2	Height	.275	.176
β_3	Hour	-.096	ABSENT
β_4	Temperature	ABSENT	ABSENT

6.3.3 Activity

The monkeys are most vigilant whilst resting and eating from pouches (a sub-category of resting) (Figure 6.3). Lower vigilance levels are observed whilst feeding and being groomed and very low levels of vigilance are apparent whilst grooming other individuals.

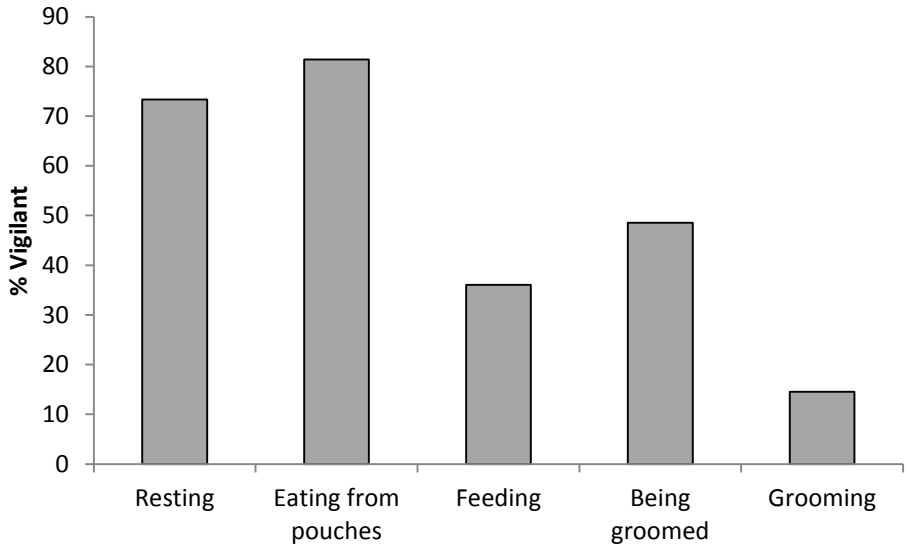

Figure 6.3 Proportion of time spent vigilant within all the activity categories.

When compared to all the other activity types the monkeys showed the highest mean glance rate whilst feeding, of approximately 7 attention shifts per minute (Figure 6.4). This is approximately 1.7 times more often than whilst resting and eating from pouches, 2 times more often than when being groomed and 3.5 times more often than when grooming another individual. The results indicate that when feeding the monkeys spend a relatively low proportion of their time vigilant; whilst considerably increasing their glance rate. Whilst resting and eating from pouches the monkeys have a lower glance rate compared to feeding, but higher proportion of time vigilant. When involved in grooming the monkeys spend a relatively low amount of their time vigilant and also have a lower glance rate compared to when engaged in other activities.

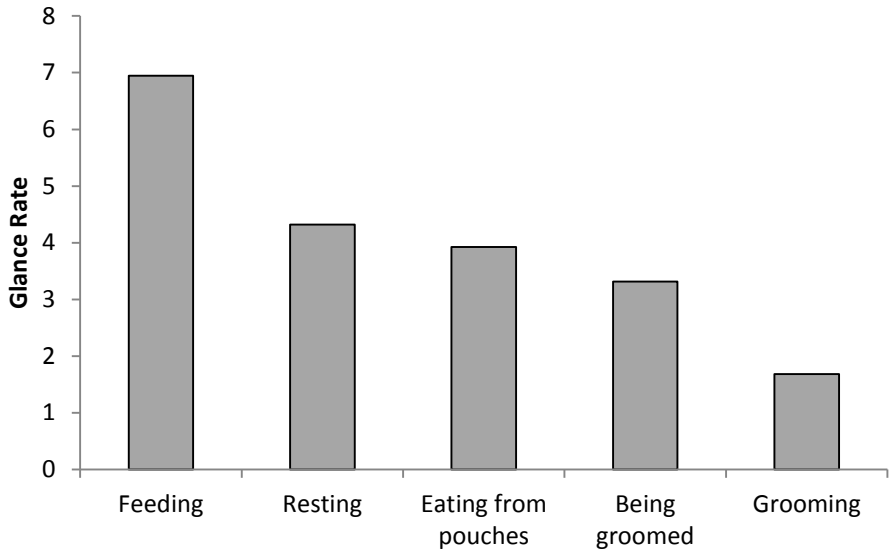

Figure 6.4 Mean glance rates (number of attention shifts per minute) during different activities.

6.3.4 Nearby conspecifics

The results show that time spent vigilant decreases as the number of nearby individuals increases (Figure 6.5). There is an overall decrease of approximately 20% vigilance as the number of individuals within 5 metres of the focal individual increases from 0 to 10.

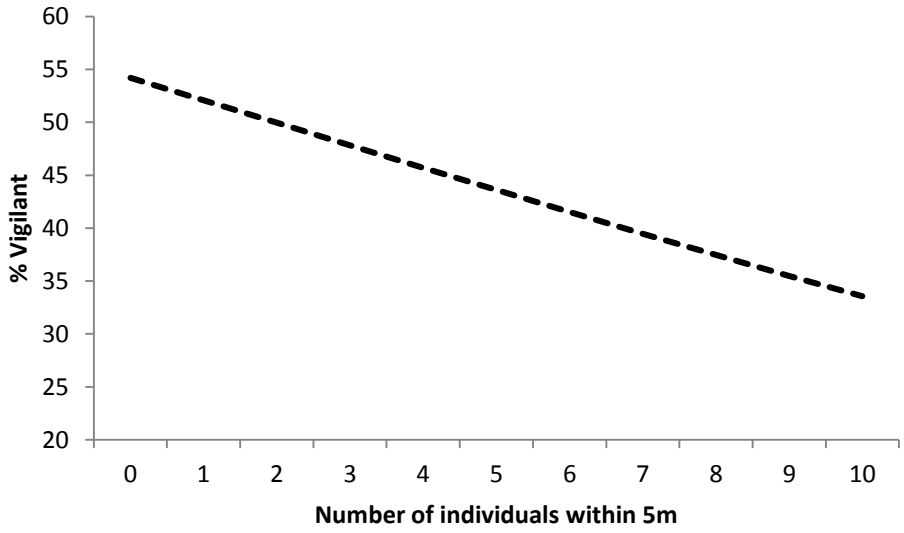

Figure 6.5 Effect of number of nearby individuals on time spent vigilant.

Number of nearby individuals have very little effect on glance rate, with an overall increase of just 0.19 attention shifts per minute from 0 to 10 individuals within 5 metres (Figure 6.6). The results mentioned show that nearby individuals appear to have important effects on proportion of time vigilant, with a sizeable decrease in vigilance as number of nearby individuals increases; however, the effect of nearby individuals appears to have no measurable effect on glance rate.

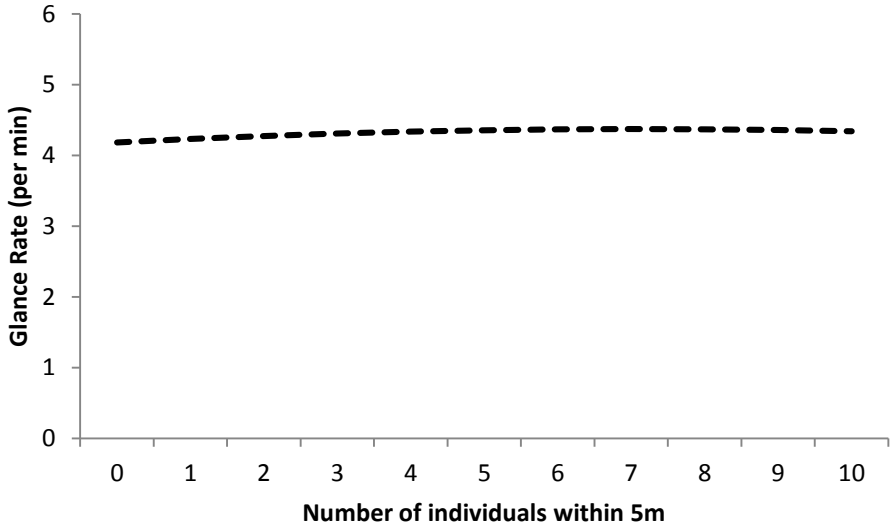

Figure 6.6 Mean glance rates (number of attention shifts per minute) with varying numbers of individuals within 5m.

6.3.5 Height

Vigilance increases by over 10% as individuals move from 0 to 10m (Figure 6.7). Height has a similar effect on overall vigilance within both the resting and feeding categories (Figure 6.8). This indicates that there is no measurable interaction between the effects of height and activity type on proportion of time vigilant.

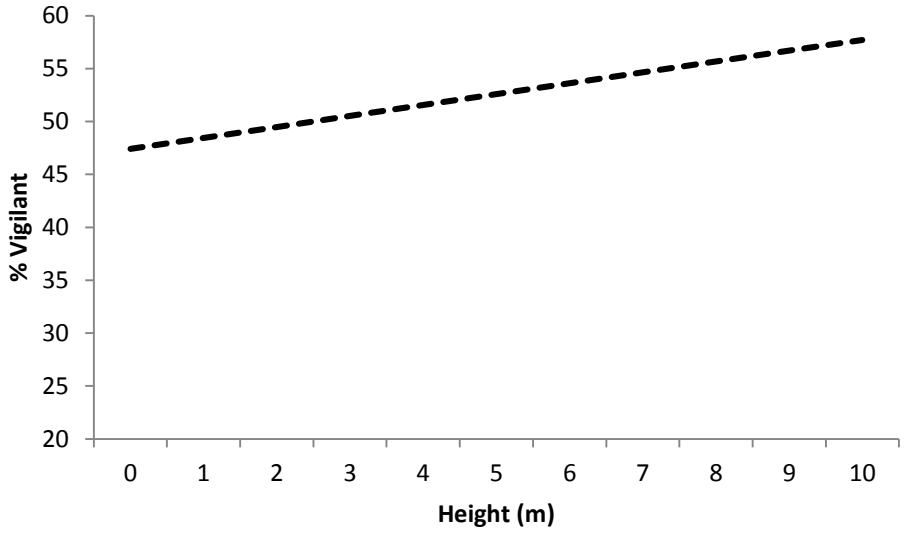

Figure 6.7 Effect of height of focal individual on proportion of time vigilant.

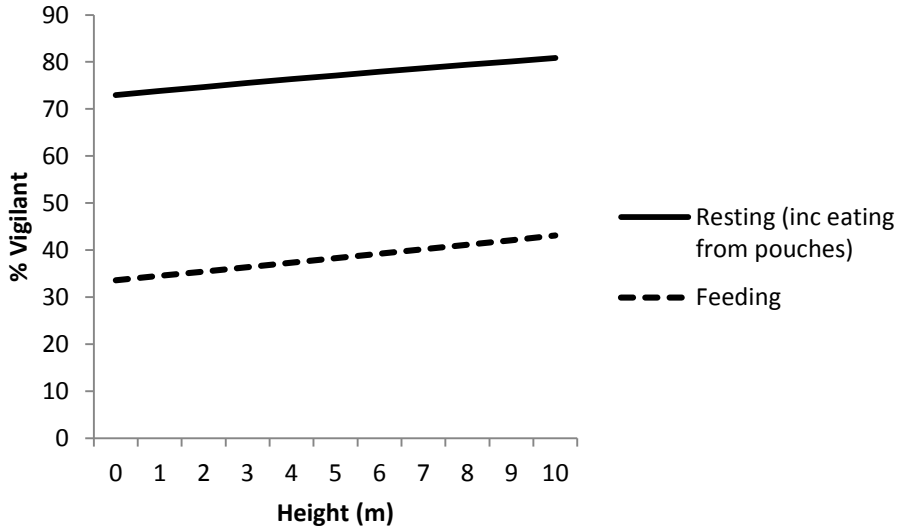

Figure 6.8 Effect of height of focal individual on proportion of time vigilant within two different activity categories

There is a sizeable increase in observed glance rate as height of the focal individual decreased, with a mean glance rate of 2.4 attention shifts per minute when at 10 metres to 5.4 per minute at 0 metres (Figure 6.9). Similarly to the effect on proportion of time vigilant, there appears to be no interaction between height and activity type in this instance (Figure 6.10).

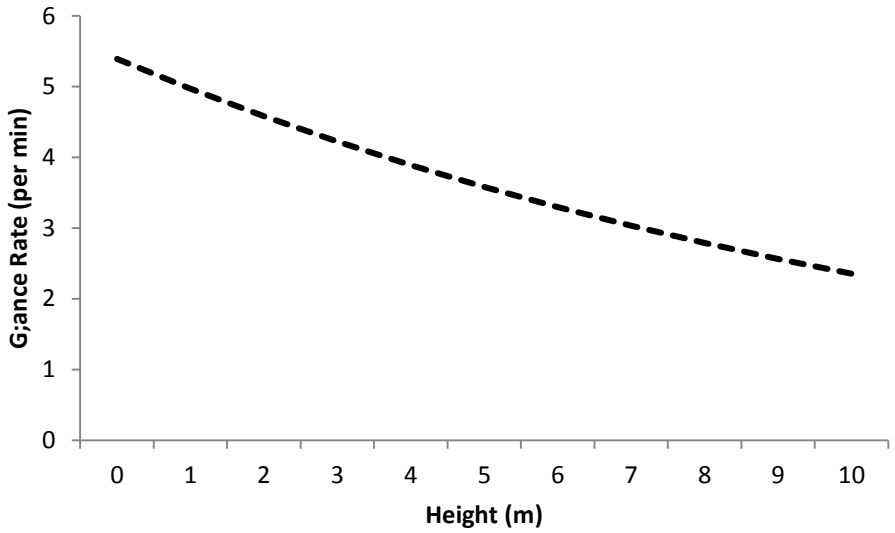

Figure 6.9 Mean glance rates (number of attention shifts per minute) at various heights.

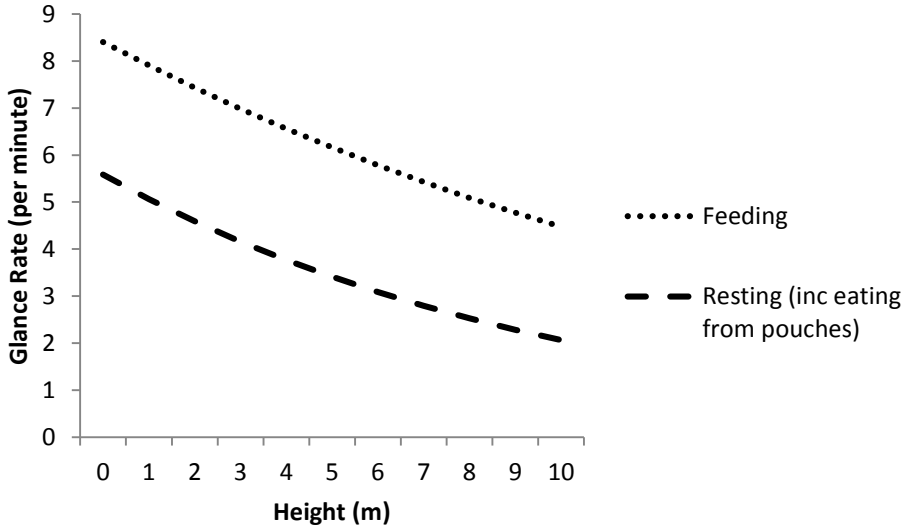

Figure 6.10 Mean glance rates (number of attention shifts per minute) at various heights within two different activity categories.

6.4 Discussion

Remaining vigilant for predators is an essential component of the anti-predation strategies of all primate species (Treves 2000). However, primates must balance the foraging/vigilance trade-off in order to collect enough resources to survive,

whilst also avoiding the mortality risk predation poses (Brown 1999). This study presents a highly detailed multivariate investigation into how behavioural factors such as activity type, height in trees and conspecific proximity can affect the vigilance behaviour of an arboreal monkey species, both in terms of proportion of time vigilant and glance rate.

The results of the study showed that the activity in which an individual engages is a key contributor to both the proportion of time vigilant and glance rate. Individuals spend approximately 40% less time vigilant when foraging than when resting; whereas glance rate when resting is approximately 30% less than when feeding. This indicates that the process of foraging requires more of an individual's attention; however, an individual still exhibits a high glance rate when feeding, most likely in an attempt to sufficiently monitor its surroundings for risks (Gluck 1987, Cowlishaw et al. 2004). Another important result indicates that as number of nearby individuals increases time spent vigilant decreases, with an average decrease of approximately 2% of time vigilant for each conspecific present within 5m. This is consistent with the hypothesis made that the presence of nearby individuals reduces overall predation risk. Finally an increase in proportion of time vigilant when higher in the canopy was observed. This is not entirely consistent with the hypothesis made that, due to potential risk from both terrestrial predators and raptors, time spent vigilant would peak when both at the top of the canopy and when at ground level. However, glance rate was much higher closer to the ground than when higher in the canopy, which suggests the potential for two peaks of predation risk.

6.4.1 Activity

Time spent vigilant was lower when feeding than when resting, a result which was expected, due to the attention requirement associated with foraging (Pulliam 1973, Treves 2000, Hill & Cowlishaw 2002). The increased glance rates observed when feeding than when resting is also consistent with the prediction made, that when at a time of predation risk, when engaged in an activity which requires its attention, an individual will maintain a higher glance rate in an attempt to monitor

its surroundings as best as possible (Gluck 1987, Cowlishaw et al. 2004). Therefore, it appears that the samangos are forced to reduce time spent vigilant in order to forage adequately; however, when foraging they attempt to counteract this vigilance disadvantage by maintaining a high glance rate. A number of primate species have been observed to decrease proportion of time vigilant whilst feeding. For example, mixed species groups of moustached and saddle-back tamarins are vigilant for approximately 90% of time resting and 35% of time feeding (Stojan-Dolar & Heymann 2010a); figures very similar to those reported in this study. Black howler monkeys have been observed exhibiting a similar pattern, with vigilance increasing by 20% of time while resting when compared to foraging (Treves et al. 2001). Yellow baboons have also been observed to significantly decrease vigilance whilst feeding (Cowlishaw 1998). In samango monkeys the same pattern has also been observed previously with decreasing vigilance correlating with increasing feeding rate (Cowlishaw et al. 2004). However, these studies failed to investigate the effect of these activities on both time spent vigilant and glance rate. This study has shown that glance rate can vary substantially when resting compared to when feeding, and that maintaining a high glance rate has the potential to be an important anti-predation vigilance strategy.

The activity which was linked to the lowest level of vigilance was grooming another individual (<20%). Grooming another individual requires the groomee's attention, and therefore, similarly to when feeding, individuals have to reduce the proportion of time they can remain vigilant. When an individual was being groomed vigilance was also relatively low (<50%). One possible reason for this relatively low level of vigilance is that it is often difficult for such monkeys to remain vigilant whilst being groomed due to the body positions they adopt (Cords 1995). It would seem logical that due to the difficulty of remaining vigilant whilst allogrooming the samangos should engage in this activity at times or in locations they consider lower predation risk. However, Cords (1995) observed the same lack of vigilance when samango monkeys engaged in allogrooming, but found no evidence of the activity occurring at safer times or in safer locations. The conclusions of the Cords study were that allogrooming must be such an important activity to the monkeys that the individuals participating accept the increased

predation risk associated with lowered vigilance rates. If this were the case in the Lajuma samangos we would expect glance rate to be high when grooming in an attempt to minimise this risk. However, this result was not observed, as the two grooming activities had the two lowest glance rates. Therefore, it is likely that the Lajuma samangos are grooming at times they consider a lower risk of predation.

6.4.2 Nearby conspecifics

It was predicted that as the number of nearby individuals increased individual vigilance would decrease, and this was the pattern observed, suggesting a decrease in risk associated with nearby conspecifics. This is a common pattern in primate studies, in species such as Thomas' langurs, which have been observed to significantly decrease vigilance with only a few individuals nearby, compared to when solitary (Steenbeek et al. 1999). Similar effects have been observed in white-faced capuchins (Rose & Fedigan 1995), black howler monkeys (Treves et al. 2001) and ursine colobus monkeys (Teichroeb & Sicotte 2012).

One possible reason for this decrease in time spent vigilant involves the foraging/vigilance trade-off. Nearby individuals might cause increased competition for food, which in turn may force individuals to increase their time feeding, reducing time available for vigilance. If this were the case the number of nearby individuals would increase the proportion of time vigilant whilst feeding; whereas, the results of the model run on samples only taken whilst feeding indicated no observable effect of number of individuals within five metres on time spent vigilant. The results therefore point towards an anti-predation hypothesis. Individuals may be able to reduce their own vigilance investment through reliance on other members of their foraging group to share the vigilance load (Pulliam 1973, Mcnamara & Houston 1992). Such strategies allow individuals to approach the foraging/vigilance trade-off differently than if they foraged solitarily. Individuals may be able to forage more efficiently because they can rely on nearby individuals, who are being vigilant, to alert them should a threat arise (Pulliam 1973). Such cooperative strategies could be made even more efficient by the use of synchronous strategies, where individuals actively take turns remaining

vigilant so others can forage in relative safety. Evidence for synchronous vigilance strategies has been observed in Defassa waterbuck (*Kobus ellipsiprymnus defassa*) (Pays et al. 2007) and eastern grey kangaroo (*Macropus giganteus*) (Pays et al. 2009); however, this type of vigilance behaviour is understudied in primates providing possible interesting future avenues for the study of vigilance synchronicity in primates.

6.4.3 Height

The results of this study indicate that time spent vigilant increases with increasing height in the canopy. This is consistent with the results from a previous chapter, which showed that samangos consider arboreal predators a higher risk than terrestrial predators (Section 5.3). Conversely, a previous study on site observed that samangos consider the ground to be a higher risk than higher in the canopy (Emerson et al. 2011), a result which seems to contradict that of this study. Many studies, which may have only considered time spent vigilant as their dependent variable, would have no explanation for such contradictory results. However, the results of this study were able to show a substantial increase in glance rate when nearer the ground than when higher in the canopy. Varying glance rates may be a compensatory strategy used when individuals are engaged in an activity which requires their attention (Gluck 1987, Cowlishaw et al. 2004), therefore, samangos may still consider predation risk to be high near the ground even though they reduce the time they are vigilant. At ground level, arboreal samangos may consider predation risk from terrestrial predators to be high and they may endeavour to minimise their time spent at this height to reduce this risk. They may not want to reduce their foraging efficiency and so instead reduce their time spent vigilant and compensate for this with a high glance rate. This theory is supported by evidence from Chapter 3 (Table 3.6), where a significant positive correlation was observed between time spent feeding and terrestriality. This indicates that the samangos increase the proportion of time spent feeding when on the ground, which may make a considerable contribution to the reduction in time spent vigilant.

Due to data being collected through direct observation of the monkeys a maximum sample height of 10m was achieved. The maximum canopy height for much of Lajuma was below 10m; however, there were areas where the canopy reached up to 20m in height (pers. obs.). Thus, whilst trends were observed in both time spent vigilant and glance rate, there is no guarantee the trends would have continued above 10m in height.

6.4.4 Statistical analysis

The aim of this study was to use a multivariate modelling approach to investigate possible intra-group effects on samango monkey vigilance behaviour, in terms of proportion of time vigilant and glance rate. However, the nature of the data collected meant that no traditional statistical tests were appropriate. Therefore, a modelling framework was constructed which considered the effects of a variety of independent variables simultaneously, without the assumption restrictions imposed by many traditional statistical tests (Pawitan 2001, Richards et al. 2011). One possible weakness in the approach used is that it did not yield p-values, a common way of determining statistical significance in results. Models were selected based on AIC score and all selected models contained effects of height and nearby individuals, indicating these factors are important determinants of vigilance behaviour (Richards 2008). Therefore, the results from the analyses show definite strong trends, for which p-values would only serve to further confirm already evident effects. Although traditional tests would have yielded p-values they would have inevitably led to a reduction in the reliability of any results caused by the breaking of their assumptions. The creation of a custom-made model, with no such statistical assumptions, allowed for the reliable computation of some interesting and original results.

6.4.5 Conclusions

This study is the first to investigate, in such detail, how the combination of a variety of behavioural factors can affect primate vigilance behaviour, both in terms of time spent vigilant and glance rate. The results of this study have

highlighted glance rates as a likely essential aspect of primate vigilance behaviour, due to the potential for a high glance rate to act as an alternative to a higher proportion of time vigilant during activities which require an individual's attention. However, the determinants of varying glance rates in primates are still poorly understood and are an element of vigilance behaviour which requires much more research.

When observing vigilance behaviour it is extremely difficult (and at times impossible) to differentiate between predator vigilance, social vigilance and time spent looking at items such as food. Therefore, caution should be applied when drawing conclusions regarding perceived predation risk based on vigilance behaviour. However, the patterns observed in this study are strongly supported by ecological theory, suggesting overall reliability.

The approach used in this chapter did not take into account changes in gaze direction, such as looking up or down. Such changes in gaze direction may be important in understanding vigilance behaviour, as an individual spending a lot of time looking downwards may indicate a high perceived risk from terrestrial predators (Peres 1993, Fichtel & Kappeler 2002). The approach presented here also does not account for potential spatial variation in vigilance behaviour. Perceived predation risk can vary spatially (Chapter 5) and so vigilance for predators may also vary spatially. These elements of vigilance behaviour will be considered in the next chapter.

Chapter 7

Spatial Variation in Vigilance Behaviour

7.1 Introduction

Optimal foraging theory dictates that animals should maximise their net energy intake by using resources in the most efficient way possible (Emlen 1966, Macarthur & Pianka 1966). If resources vary spatially this would be achieved through the strategic use of habitats to maximise food intake and therefore fitness; however, this fails to take into account the potential effect of predation risk (Kotler & Holt 1989). Predation risk may vary spatially due to variation in habitat characteristics such as cover from vegetation or accessibility of areas to predators (Mcnamara & Houston 1987, Lima 1998, Brown & Kotler 2004). A previous chapter showed that samango monkeys strategically utilise space to reduce the predation risk they encounter (Chapter 5); however, animals often employ other strategies in an attempt to reduce risk further. One of the most common anti-predator behaviours is to remain visually vigilant for predators, in an attempt to detect threats before they are able to inflict damage (Treves 2000). The previous chapter showed that samangos at Lajuma vary their vigilance behaviour as a consequence of their behavioural ecology, for example, reducing time spent vigilant whilst feeding compared to when resting (Chapter 6). This chapter will further investigate vigilance behaviour in samango monkeys through the examination of how vigilance varies spatially throughout the landscape.

Many species, including primates, have difficulty foraging and remaining vigilant simultaneously (Underwood 1982, Lima 1998, Treves 2000). Therefore, individuals are often forced to trade-off between time spent foraging and time

spent vigilant (Hill & Cowlishaw 2002). At times of low food availability individuals might need to spend more time foraging, which may increase their predation risk due to reduced vigilance potential (Gursky 2000, Hanya 2004, Guo et al. 2007). Primates must employ various anti-predation strategies in an attempt to minimise predation risk, whilst also maintaining sufficient foraging efficiency. A common anti-predator strategy is group living (Alexander 1974, van Schaik 1983) and the majority of primate species live in social groups for this reason (Clutton-Brock & Harvey 1977). Living in such groups has the potential to reduce predation risk either through the "dilution effect" (Hamilton 1971, Dehn 1990), predator deterrence (Maisels et al. 1993) or perhaps most importantly due to an increase in the number of potentially vigilant individuals (Cresswell 1994). Many primate species use alarm vocalisations to inform other group members when a threat is detected (Fedurek & Slocombe 2011). This potentially allows individuals living in groups to reduce their own vigilance load and consequently forage more efficiently. While these groups move around their landscape a number of factors are likely to contribute to a varied level of predation risk and consequently a variation in vigilance behaviour. Primates, particularly those which are arboreally adapted, are likely to have to consider how predation risk varies on both horizontal and vertical scales.

7.1.1 Spatial variation of risk

Regarding horizontal spatial variation in predation risk and vigilance one of the most comprehensively studied systems is in Yellowstone National Park, where bison (*Bison bison*) and female elk residing there display significantly higher levels of vigilance when in wolf populated areas compared to non-wolf areas (Laundre et al. 2001, Childress & Lung 2003). Nubian ibex consider cliffs a refuge and have been observed to increase time spent vigilant when further away from these refuges, suggesting a direct link between perceived predation risk and vigilance.

Some primate studies have investigated how habitat usage, which can be associated with varying levels of predation risk, can affect vigilance behaviour. Yellow baboons increase vigilance in more open habitats, which are often

associated with increased predation risk (Cowlishaw 1998) and white-faced capuchins have been observed increasing vigilance around water-holes, where they have to move away from forest cover (Rose & Fedigan 1995). However, squirrel monkeys (*Saimiri* spp.), when moving to areas of lower vegetative density, which provides better access for eagle predators, have not been observed to increase their vigilance (Boinski et al. 2003). Whilst these studies have attempted to investigate how habitat associated with different levels of risk may be linked with variation in vigilance behaviour, no previous primate study has been able to observe a direct link between perceived predation risk and vigilance.

Many arboreal primates must survive predation threats from both terrestrial predators, such as big cats, and arboreal predators, such as raptors (Peres 1993, Fichtel & Kappeler 2002). If raptor predation risk is perceived to be high then an individual may spend more time looking upwards. If risk from terrestrial predators is considered high then more time might be spent looking downwards. For example, in mixed-species groups, saddle-back tamarins spent more time scanning downwards for terrestrial threats whilst red-cap moustached tamarins spent more time scanning upwards for aerial threats, indicating complementary anti-predation strategies (Peres 1993).

For many individuals, particularly those from arboreal species, predation risk varies on a vertical scale (Wright 1998, Cooper 2006, Emerson et al. 2011, Kosinski et al. 2011). Individuals which consider risk from terrestrial predators to be important might be expected to increase time spent vigilant when lower in the canopy. Indeed such a pattern has been observed in several primate species, such as Thomas' langurs (Steenbeek et al. 1999), moustached and saddleback tamarins (Smith et al. 2004) and brown capuchin monkeys (Hirsch 2002). However, should an individual perceive risk to be higher from aerial predators, the opposite pattern would be expected and has been observed in vervet monkeys (Baldellou & Henzi 1992).

7.1.2 Visibility

We would expect the visibility within a habitat to have an effect on their vigilance behaviours. A habitat with high foliage density may provide cover from a predator but may limit an individual's ability to monitor its surroundings; high visibility may have the opposite effect. Indeed, studies have reported varying habitat visibility to have very different effects on prey animals' vigilance behaviour. For example pronghorns (*Antilocapra americana*) have been observed increasing time spent vigilant for coyotes (*Canis latrans*) when in lower visibility areas (Goldsmith 1990); whereas degus (*Octogon degus*) increase time spent vigilant whilst foraging in areas of higher visibility (Vasquez et al. 2002). The behavioural responses of the prey are likely to depend on their anti-predation strategy; in other words, whether they attempt to remain hidden from predators or try to spot them from a distance and find a refuge.

There have been a number of studies on the effect of habitat visibility on the vigilance behaviour of primates. Squirrel monkeys decrease vigilance in areas of low visibility, probably because low observable distance renders vigilance ineffective (Boinski et al. 2003). Conversely, a study investigating vervet monkeys in St. Kitts observed that vigilance increased in more dense vegetation, suggesting that low visibility reduced the vervets' ability to monitor their surroundings for potential predation threats (Chapman 1985). Similarly, after a forest fire, vervet monkeys have been observed to decrease vigilance in burned areas compared to unburned areas, with this variation being attributed to an increased ability to spot predators from greater distances (Enstam & Isbell 2002). So, if an animal prefers such areas of low foliage density due to the high visibility it confers, they may be able to reduce overall time spent vigilant (Chapman 1985, Enstam & Isbell 2002). This should leave more time available for an individual to feed, which may have important effects on its overall fitness (Hill & Cowlishaw 2002).

7.1.3 Conspecific risk

So far risk has only been discussed in terms of risk from predators but many primates also have to consider potential risks from conspecifics (Gaynor & Cords

2012). Many species of primate are territorial and edges of territories often coincide with those of rival groups (Bates 1970). Within these areas aggressive inter-group encounters often occur which can result in injury or even death (Palombit 1993, Sicotte & MacIntosh 2004). When foraging in these areas individuals may increase time spent vigilant to monitor for the potential presence of rival groups. Moustached tamarins increase time spent vigilant when in areas of home range overlap with rival groups (Stojan-Dolar & Heymann 2010a) and similarly ursine black and white colobus monkeys showed the highest levels of vigilance during inter-group encounters and when occupying areas of home range overlap (Macintosh & Sicotte 2009).

7.1.4 Samango monkeys

Samango monkeys, being an arboreal monkey species likely experience variable predation risk on both a horizontal and vertical scale, which may have important effects on spatially varying vigilance behaviour. The results of a previous chapter indicated that the samangos in Lajuma consider eagles to be a principal predation risk (Chapter 5.3). To spot eagle threats before they are able to inflict damage, members of the group must remain visually vigilant (Cords 1990, Gaynor & Cords 2012). Once a threat has been identified alarm vocalisations, including an eagle-specific call, alert other members to the imminent risk (Cords 1987, Brown 1989, Papworth et al. 2008). In an attempt to reduce risk it is expected that when in areas considered high risk of eagle predation, samangos will increase the proportion of time spent vigilant. Samango monkeys in the Kakamega Forest in Kenya, when in areas of higher perceived eagle predation risk, increase time spent looking upwards (Cords 1990). Therefore, the same pattern is expected for the Lajuma samangos.

Samango monkeys have evolved to live a predominantly arboreal lifestyle (Anapol et al. 2005) and they are likely to perceive predation risk to vary vertically. In a previous study investigating the effect of height on samango vigilance behaviour Gaynor & Cords (2012) observed proportion of time spent vigilant to increase with decreasing height. This is contrary to the results of the Lajuma samangos

which were observed to increase time spent vigilant with increasing height (Figure 6.7). These opposing results are as expected when the predators at each site are considered. The Gaynor and Cords study was conducted in the Kakamega Forest in Kenya where the main samango predators are terrestrial; however, the main predators at Lajuma are aerial. A pattern observed by Emerson et al. (2011), when studying the Lajuma samangos is more difficult to explain. Using giving-up density experiments, Emerson et al. (2011) concluded that the Lajuma samangos perceive risk to be higher when closer to the ground. At first sight it appears that the two studies on the same study population conflict. In an attempt to explain this variation an element of vigilance behaviour yet to be discussed must be considered, which is glance rate. The results from the previous chapter showed that while time spent vigilant decreased, individuals increased glance rates considerably when nearer the ground (Chapter 6). A high glance rate may allow an individual to maintain an adequate level of vigilance, even when engaged in activities which require a large proportion of its attention (Gluck 1987, Cowlishaw et al. 2004). If the samangos perceive risk from terrestrial predators to be high when foraging near the ground, they may attempt to minimise time spent foraging at such heights. However, foraging as quickly as possible reduces time available for vigilance (Hill & Cowlishaw 2002) so they maintain a high glance rate. These results therefore suggest the samangos may experience high risk both at ground level from terrestrial predators and higher in the canopy from aerial predators.

The results of a previous chapter indicated that the Lajuma samangos prefer to use areas of taller canopy (Section 5.3). As mentioned above, the samangos actively avoid areas they consider high risk of predation (Section 5.3), suggesting that they perceive areas of tall forest (mean height >10 m) to be of a lower overall predation risk than areas with lower canopy height. This seems counter-intuitive given the previous analysis showed a trend of increasing vigilance with height of focal individual (Section 6.3); however, that analysis did not account for canopy height. The analyses used in this chapter will account for canopy height variation, and due to samangos' arboreal nature it is expected that vigilance will decrease with increasing canopy height.

The samangos in this study prefer to utilise areas of high understory visibility (Section 5.3). This preference may be due to increased visibility making vigilance for predators more effective, because individuals are able to detect predators from further away. This may cause individuals to reduce their time vigilant, as they can monitor their surroundings easier (Chapman 1985, Enstam & Isbell 2002). However, eagle hunting benefits from low foliage density to allow them to fly through the canopy (Boinski et al. 2003). High foliage density may then provide cover from predators, reducing risk and reducing the time devoted to vigilance. High foliage density has also been observed to make vigilance ineffective, leading squirrel monkeys to reduce vigilance in low visibility areas (Boinski et al. 2003). Therefore, it is difficult to make predictions about the potential links between spatially varying visibility and vigilance behaviour.

Samango monkeys are territorial, often engaging in aggressive encounters with rival groups, which can lead to injury or even death (Lawes & Henzi 1995). The only previous samango study to investigate possible effects of risk from rival groups on vigilance behaviour observed that vigilance increased significantly during inter-group encounters, although the potential spatial effect of inter-group encounter risk was not investigated (Gaynor & Cords 2012). Based on the results of this previous study it is expected that the individuals in the study group will increase time spent vigilant when in areas of perceived inter-group encounter risk.

7.1.5 Objectives

The main aim of this chapter is to investigate the spatial effect perceived predation risk can have on samango monkey vigilance behaviour. Previous results have shown that the samangos avoid areas they consider high risk of eagle predation risk (Chapter 5) and it is expected that this effect will significantly influence vigilance behaviour. The chapter will test the following predictions:

1. Time spent vigilant will increase when in areas of higher perceived eagle predation risk.

2. Time spent looking upwards will increase when in areas of higher perceived eagle predation risk.
3. Time spent vigilant will decrease when residing in areas of tall forest.
4. Time spent vigilant will increase when in areas of higher risk of inter-group encounters.

This study is the first to use dedicated spatial statistical models to investigate the factors which may influence the spatial variation in primate vigilance behaviour. Such models are specifically designed to account for spatial autocorrelation, a problem which can arise in these types of studies (Dutilleul 1993, Dormann et al. 2007).

7.2 Methods

7.2.1 Study Site

The study site was the Lajuma Research Centre, located in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). The most notable potential predators on site include leopard; crowned eagle, African black eagle and the African rock python. Furthermore, there are several species of venomous snakes present which, whilst they do not prey on samangos, still pose significant mortality threats and therefore may affect vigilance behaviour. For a comprehensive description of the study site see Section 2.2.

7.2.2 Study species

Samango monkeys are primarily frugivorous (Lawes 1991), medium sized, arboreal guenons. Group sizes range from 4-65 (Butynski 1990, Beeson et al. 1996, Smith et al. 2008, Houle et al. 2010, Lawes et al. 2011). Samangos have a variety of vocalisations, with a number classed as alarm vocalisations (Marler 1973, Brown 1989). These include an alarm call which has been well documented

as referentially specific to aerial threats such as raptors (Brown 1989, Papworth et al. 2008).

7.2.3 Data collection

A habituated samango group of approximately 40 individuals were observed over a 16 months period (Oct 2009-Dec 2010), with vigilance data collected in the last 11 months. Vigilance data were collected using 5 minute continuous focal samples. Vigilance type was separated into eight categories (for descriptions see Table 6.1). A separate category was used to indicate moving, due to the difficulty in recording accurate vigilance data when the focal individual was not stationary. A glance period was defined as the amount of time attention remained within a single vigilance category. Each time the focal individual's vigilance category changed this was recorded, along with the amount of time each glance period lasted. The location was recorded at the beginning of each sample using a GPS (Garmin GPS 60CSX).

At the beginning of each sample, data recorded for the focal individual were: name, time, activity type, height and number of individuals within 5m. The activity types used were: resting, feeding, eating from pouches, grooming, being groomed and other socialising (e.g., playing, fighting). During the sample each change in activity type was noted immediately, along with the time. Once a minute a note was made of any changes in the other behavioural categories (height of focal individual, number of individuals within 5m, activity type), as it was impossible to record changes in these instantaneously while also accurately monitoring vigilance behaviour. For a more detailed description of these methods see Section 6.2.3. Data on perceived eagle predation risk, inter-group encounter risk, food availability, visibility, canopy height and habitat type variation were extracted from spatially explicit data sets used in Chapter 5.

7.2.4 Statistical analysis

Vigilance data in the categories "unknown" and "moving" were excluded from the dataset and the sample duration was recalculated. The vigilance data in each sample were then converted into proportion of time in each vigilance category. An attention shift was defined as a change in vigilance category and glance rate was calculated as "mean attention shifts per minute". These data were coupled with the locations of the samples (Figure 7.1) to allow for spatial interpretation.

The mean height of the focal individual and number of nearby individuals (number of juveniles or adults within 5m of the focal individual) were calculated for each sample. At each sample location data on fruit availability, visibility, mean canopy height, habitat type, eagle predation risk and inter-group encounter risk were extracted from the datasets used in Chapter 5.

Through kriging interpolation (Cressie 1990), using the kriging tool in ArcGIS, "landscapes of vigilance" were created showing the spatial distribution of each vigilance category and glance rate. The search radii for the kriging analyses were selected based on the number of points achieving minimum root mean squared error (Salih et al. 2002). The landscapes of vigilance represent a purely visual representation of the spatial variation of the different vigilance behaviours and no data were extracted from the landscapes to be used in further analyses.

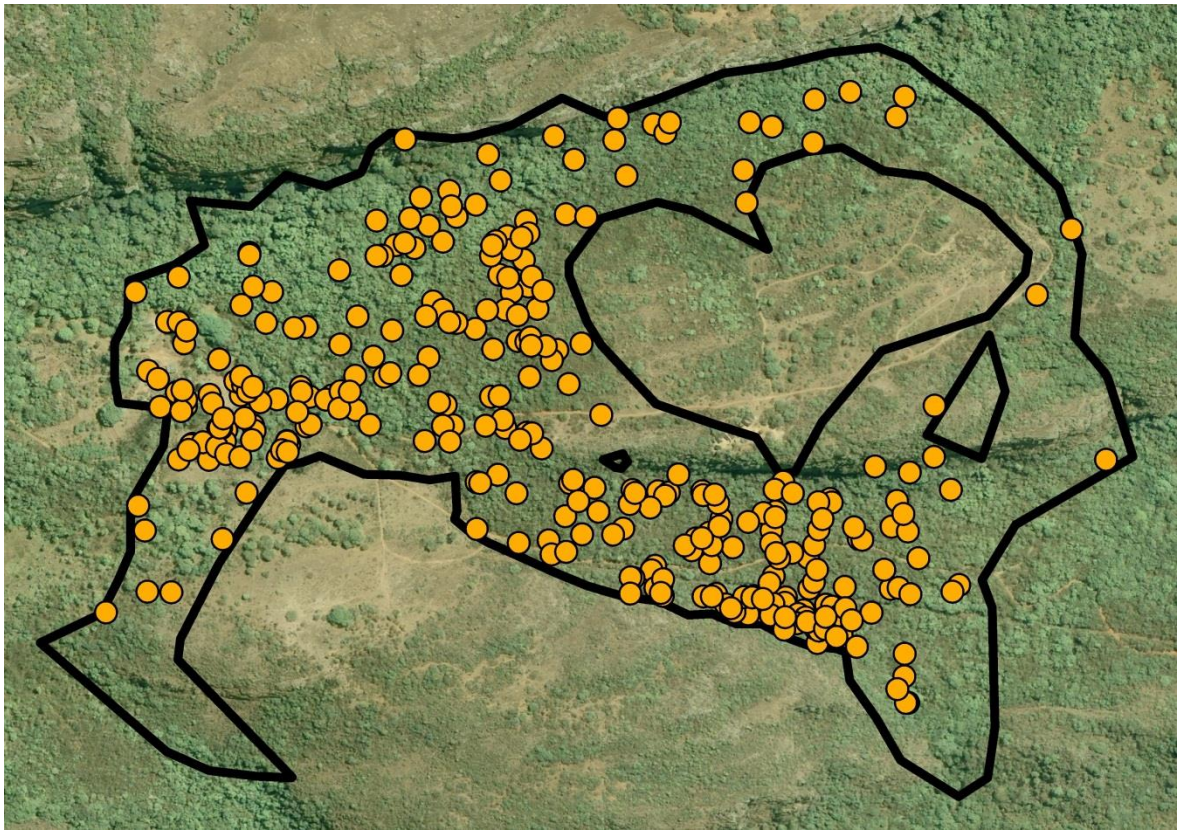

Figure 7.1 Locations of the continuous focal samples within the monkey home range (n = 332).

Global Moran's *I* values indicate a low level of spatial autocorrelation for the majority of variables (Table 7.1). Nevertheless, spatial autocorrelation within the variables was accounted for using exploratory Pearson's correlation analyses with adjusted degrees of freedom (Dutilleul 1993). The majority of samples (317/332) were situated in two habitat types (tall forest and short forest) and so habitat types were excluded from this analysis.

One-way ANOVA analyses were used to aid visual interpretation of the potential relationships between the different vigilance categories and perceived eagle risk, number of nearby individuals, height of focal individual. The independent variables were separated into distinct groups representing different levels of magnitude (Table 7.2). Such an analysis is unable to take into account spatial autocorrelation and so was only used to further investigate existing relationships from the spatial analyses.

Table 7.1 Global Moran's *I* scores for all variables included in the analyses. A figure around ±1 signifies strong positive/negative autocorrelation; a figure close to 0 means no autocorrelation (Ripa 2000).

Variable	Global Moran's *I*
Dependent variables	
Total Vigilance	.015
Look-up	.034
Look-down	-.015
Scan	.027
Glance Rate	.025
Independent variables	
Eagle Risk	.189
Ind. Height	.004
Neighbours	.062
Fruit availability	.398
Visibility	.45
Canopy Height	.902
Inter-group Risk	.191
Habitat Type	.324

Table 7.2 Independent variables used in one-way ANOVA analysis, including the sample size within each group. Eagle risk figures take from eagle landscape of fear (Figure 5.11).

Eagle Risk	N	Neighbours	N	Height	N
Low (<.05)	203	0-1	179	0-2	96
Medium (.05-.1)	95	2-4	132	2-5	196
High (.1-.2)	22	5+	21	6+	40
Very High (>.2)	12				

To investigate the overall effect of each independent variables on each vigilance category and glance rate simultaneously, five mixed regressive-spatial regressive (or lagged predictor) models were used. All the data did not meet the normality assumptions of the models despite several attempts at transformations (Figure 7.2). Skewness and excess kurtosis figures are displayed in Table 7.3. A rule of thumb for skewness or excess kurtosis is a score of more than ±1 is considered

strongly non-normally distributed (Fife-Schaw et al. 2006). Therefore, the results indicate that all but the "overall vigilance" category data were non-normally distributed. Many parametric tests are robust enough to handle such a lack of normality in the data (Hubbard 1978) and the parametric model was still used, but caution is required when interpreting the data. Models were selected based on the two-step AIC criteria selection method described by Richards (2008).

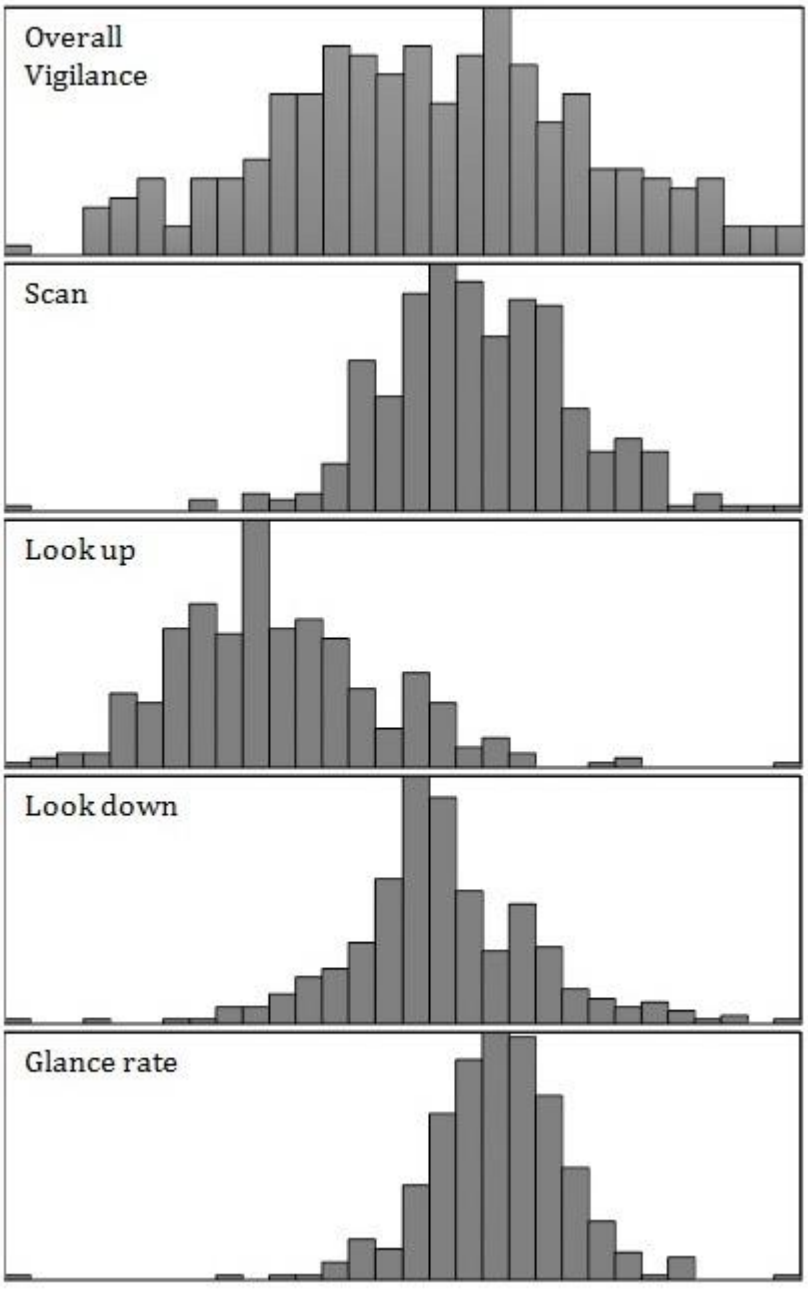

Figure 7.2 Residual distributions of the five mixed regressive-spatial regressive vigilance models.

Table 7.3 Skewness and excess kurtosis figures of the residuals from the five mixed regression-spatial regression vigilance models.

Model	Skewness	Excess Kurtosis
Overall Vigilance	.005	-.394
Scan	-.162	1.757
Look-up	.738	1.658
Look-down	.102	2.045
Glance rate	-.79	6.303

7.3 Results

7.3.1 Landscapes of vigilance

The landscapes of vigilance indicate some interesting patterns of vigilance behaviour (Figure 7.3). The landscapes for overall vigilance, scanning and looking upwards all show a definite peak of proportion of time vigilant in the north-west section of the home range; whereas, time spent looking downwards and glance rate show no such peak in this area. The highest glance rates are in the eastern section of the home range.

7.3.2 Linear correlation analysis

Overall proportion of time spent vigilant shared significant positive relationships with perceived eagle predation risk and height of focal individual and shared a significant negative relationship with number of nearby individuals (Table 7.4). These relationships can also be seen within the grouped data (Figure 7.4), with the one-way ANOVA analyses showing the same significant relationships with eagle risk ($F = 3.020$, $p = .03$), nearby individuals ($F = 7.688$, $p = .001$), and height of focal individual ($F = 6.497$, $p = .002$). None of the other independent variables correlated significantly with overall time vigilant. Similarly to overall time vigilant,

proportion of time scanning was significantly positively correlated with perceived eagle predation risk and negatively correlated with number of nearby individuals; however, time spent scanning shared no other significant relationships with the remaining independent variables. Time spent looking upwards shared the same patterns as time spent scanning, except no significant relationship with height of individual and a significant positive relationship with canopy height. The relationships between time spent looking upwards and eagle predation risk ($F = 4.251$, $p = .006$) and number of nearby individuals ($F = 9.944$, $p = <.001$) can be seen within the grouped data (Figure 7.5). Time spent looking downwards did not have a significant correlation with perceived eagle predation risk; however, showed a significant positive relationship with height of focal individual and significant negative relationship with number of nearby individuals. Time spent looking downwards shared no significant relationships with the other independent variables. Finally, glance rate correlated significantly negatively with both number of nearby individuals and height of focal individual; but shared no other significant relationships.

7.3.3 Spatial regression analysis

According to the mixed regressive-spatial regressive models used, overall time spent vigilant no longer shared a significant relationship with perceived eagle predation risk (Table 7.5), although the significant relationships with number of nearby individuals and height of focal individual remained. Time spent scanning no longer shared any significant relationships with any of the independent variables. The results for time spent looking upwards remained the same as for the linear correlation analysis in that there was a significant positive relationship with eagle predation risk, a significant negative relationship with number of nearby individuals and no significant relationship with height of focal individual. Similarly to the correlation analysis time spent looking downwards shared no significant relationship with perceived eagle predation risk, but a significant positive relationship with number of nearby individuals. However, the two analyses differ in that height of focal individual did not share a significant relationship with time spent looking downwards. Finally glance rate shared a

significant negative relationship with number of nearby individuals, but no other significant relationships. Visibility, food availability, habitat type, canopy height or inter-group encounter risk as independent variables were dropped from all selected models based on AIC_c score indicating no important effects on vigilance behaviour.

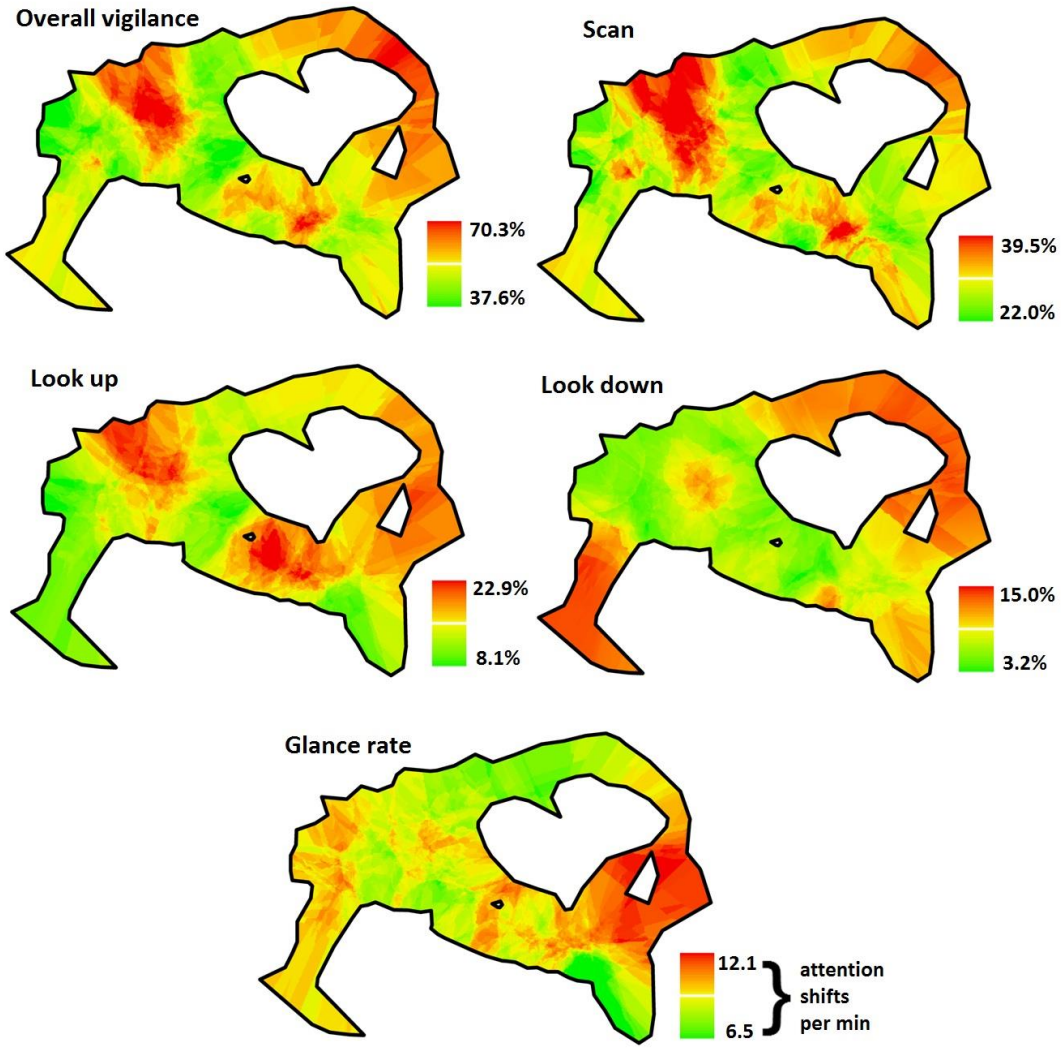

Figure 7.3 Landscapes of vigilance interpolations detailing spatial distribution of mean proportion of time spent in different vigilance categories and glance rate, based on data from focal continuous sampling.

Table 7.4 Results of Pearson's correlation analyses (*n*=332) based on geographically corrected degrees of freedom (Dutilleul 1993) between vigilance categories/glance rate and perceived eagle risk (Eagle Risk), inter-group encounter risk (I.E. Risk), fruit availability (Fruit Avail) canopy height, visibility, height of focal individual (Ind. Height) and number of nearby individuals (Neighbours). Statistically significant relationships (*P* = <.05) are displayed in bold.

	Overall Vigilance			Scan			Look-Up		
Variables	**Pearson *r***	**Corrected *df***	**p**	**Pearson *r***	**Corrected *df***	**p**	**Pearson *r***	**Corrected *df***	**p**
Eagle Risk	.113	308.962	**.046**	.124	353.257	**.019**	.136	252.987	**.03**
I.E. Risk	-.022	357.813	.675	.046	387.567	.361	-.048	314.394	.397
Fruit Avail	-.046	241.171	.476	-.016	319.384	.781	-.064	171.291	.401
Canopy Height	.097	289.093	.098	.066	399.792	.186	.153	186.658	**.036**
Visibility	-.024	307.894	.671	.014	551.028	.748	-.069	179.841	.357
Ind. Height	.171	314.703	**.002**	.063	329.982	.252	.026	299.726	.659
Neighbours	-.217	319.959	**<.001**	-.136	335.441	**.012**	-.245	295.213	**<.001**

	Look-Down			Glance Rate		
Variables	**Pearson *r***	**Corrected *df***	**p**	**Pearson *r***	**Corrected *df***	**p**
Eagle Risk	-.043	328.77	.433	.094	339.63	.083
I.E. Risk	-.071	343.98	.19	.02	346.584	.709
Fruit Avail	-.012	555.856	.77	-.054	277.985	.367
Canopy Height	-.02	316.382	.716	-.005	361.986	.927
Visibility	.003	361.603	.953	.041	373.963	.432
Ind. Height	.306	331.184	**<.001**	-.165	317.4	**.003**
Neighbours	-.114	326.984	**.039**	-.145	336.629	**.008**

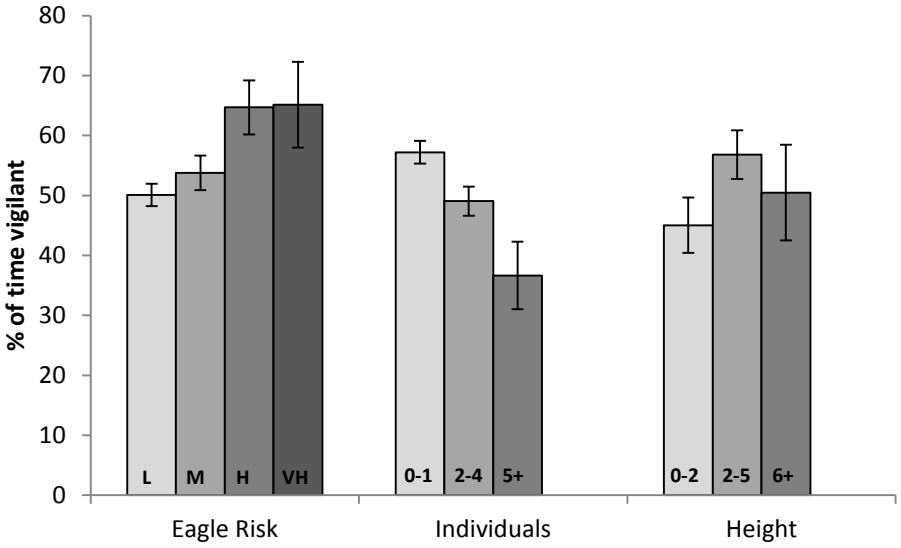

Figure 7.4 Patterns of overall time spent vigilant within different grouped variables. Eagle risk groups were: low risk (L), medium risk (M), high risk (H) and very high risk (VH). Other variables are number of individuals within 5m (Individuals) and Height of focal individual in metres (Height). Error bars display standard error.

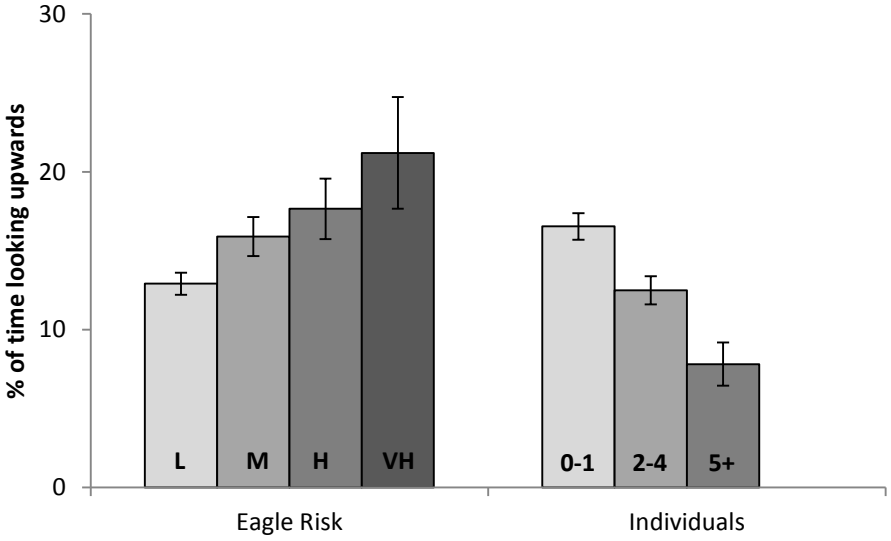

Figure 7.5 Patterns of time spent vigilant within different grouped variables. Eagle risk groups were: low risk (L), medium risk (M), high risk (H) and very high risk (VH). Other variables are number of individuals within 5m (Individuals). Error bars display standard error.

Table 7.5 Results of five mixed regressive-spatial regressive models, with response variables vigilance categories/glance rate vs. eagle risk, individual height, number of nearby individuals.. Terms: *γ,* spatial cross-regressive parameter; B, unstandardised regression parameter; *β*, standardised regression parameter, *ρ*, spatial autoregressive parameter. Statistically significant (*P* = <.05) are displayed in bold.

Overall Vigilance

Predictor	B	*β*	SE *β*	*γ*	SE *γ*	t (*β*=0)	p
Eagle Risk	.04	.026	.077	.961	.583	.514	.608
Ind. Height	.212	.222	.05	.961	3.719	4.213	**<.001**
Neighbours	-.289	-.273	.056	.961	2.456	-5.167	**<.001**

N=332 **R^2 =** .158 ***ρ*=**.961 **SE *ρ*=** 3.11 **AIC_c=** 3279.1

Scan

Predictor	B	*β*	SE *β*	*γ*	SE *γ*	t (*β*=0)	p
Eagle Risk	.023	.015	.085	.961	.583	.27	.788
Ind. Height	.038	.039	.055	.961	3.719	.681	.496
Neighbours	-.118	-.109	.061	.961	2.456	1.917	.056

N=332 **R^2 =** .016 ***ρ*=**.961 **SE *ρ*=** 3.301 **AIC_c=** 3019.8

Look-Up

Predictor	B	*β*	SE *β*	*γ*	SE *γ*	t (*β*=0)	p
Eagle Risk	.13	.088	.076	.961	.583	1.699	**.09**
Ind. Height	-.044	-.048	.05	.961	3.719	-.887	.376
Neighbours	-.349	-.34	.055	.961	2.456	-6.31	**<.001**

N=332 **R^2 =** .122 ***ρ*=**.961 **SE *ρ*=** 2.707 **AIC_c=** 2661.9

Look-Down

Predictor	B	*β*	SE *β*	*γ*	SE *γ*	t (*β*=0)	p
Eagle Risk	-.13	-.079	.079	.961	.583	-1.639	.102
Ind. Height	.459	.446	.052	.961	3.719	8.883	**<.001**
Neighbours	-.102	-.089	.057	.961	2.456	-1.772	.077

N=332 **R^2 =** .235 ***ρ*=**.961 **SE *ρ*=** 4.186 **AIC_c=** 2645.2

Glance Rate

Predictor	B	*β*	SE *β*	*γ*	SE *γ*	t (*β*=0)	p
Eagle Risk	.13	.081	.084	.961	.583	1.546	.123
Ind. Height	-.317	-.316	.055	.961	3.719	-5.816	**<.001**
Neighbours	-.065	-.059	.061	.961	2.456	-1.076	.283

N=332 **R^2 =** .102 ***ρ*=**.961 **SE *ρ*=** 2.776 **AIC_c=** 2029.3

7.4 Discussion

The aims of this study were to investigate the factors which might drive spatial variation in vigilance behaviour. The key result to emerge from the analyses is that spatial variation in eagle perceived predation risk has a significant effect on samango monkey vigilance behaviour, particularly the proportion of time spent looking upwards. When in areas considered higher risk of eagle predation, the monkeys spent more time looking upwards, which is consistent with an anti-predatory vigilance response to a potential arboreal threat (Cords 1995). The number of nearby individuals was also an important correlate of vigilance behaviour; as the number of nearby individuals increased, time spent vigilant and glance rate decreased. The height of focal individual had some shared important relationships with other variables, including a positive relationship with overall time spent vigilant and a negative relationship with glance rate. There were no significant effects of visibility, food availability or habitat type on vigilance behaviour, and the only effect of canopy height was a significant positive relationship observed in the correlation analysis, although no effect of canopy height was observed in the multivariate analysis.

7.4.1 Determinants of vigilance behaviour

The effect of perceived eagle predation risk on overall time spent vigilant and time spent looking upwards was as predicted. Although some primate studies have suggested links between habitat usage and vigilance (Rose & Fedigan 1995, Cowlishaw 1998), this study is the first to present a direct link between spatially varying predation risk and vigilance behaviour. It is known that samangos avoid using areas where they consider eagle predation risk to be high, even though there may be beneficial resources in those areas (Section 5.3). Therefore, the results here show that even when actively avoiding the higher risk areas, perceived eagle risk still has a significant effect on the vigilance behaviour of the monkeys. This suggests that it is important to understand and control for the potential effect of spatially varying predation risk when considering anti-predator behaviour. Varying vigilance

behaviour in relation to perceived eagle predation risk may be an important strategy in regard to samango foraging efficiency. By lowering time spent vigilant when in areas considered lower risk of predation, this potentially creates more time to spend foraging (Hill & Cowlishaw 2002). Therefore, by varying their vigilance in such a way, the samangos are not only improving fitness by reducing predation risk when in high risk areas, but are also improving fitness through efficiently balancing their foraging behaviour.

Another important determinant of proportion of time spent vigilant in samangos appears to be the effect of nearby individuals. There were consistent significant negative relationships between number of individuals within 5m and time spent vigilant. This result is confirmed by the findings of a previous analysis (Figure 6.5) and has been observed in a variety of different primate studies (van Schaik & van Noordwijk 1989, Rose & Fedigan 1995, Cowlishaw 1998, Treves 1998, Steenbeek et al. 1999, Treves et al. 2001, Smith et al. 2004, Stojan-Dolar & Heymann 2010a, Teichroeb & Sicotte 2012). One possible reason for this decrease in time spent vigilant involves the foraging/vigilance trade-off. Nearby conspecifics might cause increased competition for food, which in turn may force individuals to increase their time feeding, reducing time available for vigilance. If this were the case the number of nearby individuals would increase the proportion of time vigilant whilst feeding and the results of a previous analysis indicated no observable effect of number of individuals within 5m on time spent vigilant when feeding (Section 6.3.2). The results therefore point towards a reduction in risk caused by increased group density. This may be due to “dilution effect” (Hamilton 1971, Dehn 1990) or by predator deterrence (Maisels et al. 1993); however, perhaps the most likely reason for the effect is the sharing of the vigilance load between nearby individuals (Mcnamara & Houston 1992).

A previous analysis showed time spent vigilant increased with height, with strong effects on glance rate (Section 6.3.5). The results of the analyses in this study suggest the same pattern, of increasing vigilance and decreasing glance rate with height. As

samangos consider eagles an important predation risk we would expect them to increase vigilance whilst in the upper canopy (Baldellou & Henzi 1992). An increased glance rate may be a response to increased risk from predators at times when other activities require their attention (Gluck 1987, Cowlishaw et al. 2004). Time spent on the ground and time spent feeding are positively correlated (Table 3.6), so increasing time feeding on the ground may reduce time available to spend vigilant. These findings suggest that the increased glance rate might be a response to the increased risk of predation from terrestrial predators when nearer the ground.

The three effects, of perceived eagle predation risk, nearby individuals and height of focal individual appear to be important determinants of samango monkey vigilance behaviour. Therefore, an option for samangos, when residing in areas considered a high risk of eagle predation, may be for them to increase group density. This would potentially allow individuals to minimise their own need to increase time spent vigilant, without causing risk to increase. Evidence has been found for such a pattern in elk (Proffitt et al. 2012), but as far as I am aware such a link has yet to be investigated in any primate species, and presents an interesting potential avenue for future research.

7.4.2 Non-determinants of vigilance behaviour

A prediction was made that the samango monkeys would consider areas of tall forest safer and therefore reduce vigilance, but the results showed no evidence of such a relationship, in fact the only significant relationship observed in the correlation analyses indicated an increase in time spent looking up when in areas of taller canopy. However, as canopy height was dropped from the spatial regression analysis, there is unlikely to be a direct link between canopy height and time spent looking upwards, suggesting a Type I error in the correlation analysis. The most likely reason for this error is that focal individuals were only observed up to a maximum height of 10m due to constraints on visibility. In areas of tall forest the top of the canopy is more likely to be higher than the focal individual; therefore there is more foliage for them to look

up at when searching for items such as food. The lack of effect of canopy height on vigilance behaviour suggests that predation risk does not vary with varying canopy height. There are a number of possible reasons for this; firstly because of their ability to fly, and therefore quickly change height, canopy height may have little effect on the ability of eagles to hunt. Secondly, if there is increased risk of eagle predation in areas of taller canopy, then the increased risk of terrestrial predation in areas of shorter canopy (Jaffe & Isbell 2009) may mean the two effects cancel each other out. If there is a link between time spent looking upwards and canopy height, as suggested by the correlation analysis, then these explanations would be analogous.

The results of the analyses indicated no observable effect of inter-group encounter risk on samango vigilance behaviour, a result which differs from what was predicted. Samangos have a variety of different vocalisations, such as the male's "boom" call which can be heard up to one kilometre away (Brown 1989). "Boom" calls are used regularly by males (pers. obs.) and are one of many vocalisations which can be heard over a substantial distance. With this in mind it seems unsurprising that time spent vigilant did not increase when in areas of higher likelihood of inter-group encounters. Such vocalisations are likely to travel further distance than the maximum visually detectable distance. Therefore, remaining visually vigilant for rival groups is likely to be a wasteful activity. This suggestion highlights a possible future study topic involving spatial variation in vocalisations; potentially investigating whether individuals become quieter when in or near another group's home range. To the best of my knowledge no previous primate study has investigated such a topic.

The results indicated that varying visibility had no observable effect on vigilance behaviour, either in terms of time spent vigilant or glance rate. Low foliage density may increase the effectiveness of vigilance, contributing to a reduction in time spent vigilant (Chapman 1985, Enstam & Isbell 2002). However, low foliage density may reduce cover, improving a predator's ability to hunt (Boinski et al. 2003) or reduce an individual's camouflage (Tchabovsky et al. 2001). Such effects from varying visibility may cancel each other out, contributing to the lack of visibility effect on

samango vigilance behaviour. A second possible explanation may be a weakness in the methods used to calculate visibility, which only give a measurement of understory visibility (<2m high, see Section 2.4.5). The problem lies with trying to make conclusions regarding behaviours occurring higher in the canopy. Therefore, caution has to be used when attempting to draw strong conclusions regarding visibility in this instance.

7.4.3 Statistical analysis

When analysing spatially variable ecological data, spatial autocorrelation is a problem which often needs to be addressed, mainly due to the increased risk of Type I errors (Dormann et al. 2007). This investigation utilised analyses specifically designed to account for spatial autocorrelation, therefore increasing the reliability of the results being obtained. However, the spatial regression models did show relatively low R^2 scores for similar analyses. Such a pattern is to be expected when analysing vigilance behaviour, due to high variation within the response variables and the huge number of behavioural and environmental factors which are likely to affect vigilance (Treves 2000), all of which would be impossible to measure and analyse. Nevertheless, this highlights the importance, when studying vigilance behaviour, to utilise a multivariate analysis with as many detailed independent variables as possible. This will ensure that when attempting to interpret results, the researcher can be confident of their reliability and accuracy.

7.4.4 Conclusions

The main purpose of this study was to investigate the effect spatial variation in perceived predation risk has on vigilance behaviour. Although the spatial regression showed no effect of perceived eagle predation risk on overall vigilance, a correlation analysis showed an effect of increased vigilance in high risk areas. This study shows the importance of understanding attention direction when attempting to understand variations in vigilance behaviour. The strongest effect of eagle predation risk was on

time spent looking upwards; if vigilance was only considered in terms of overall time spent vigilant this effect would have been diluted and nearly lost. A number of primate studies have been inconclusive regarding the effect of predation risk variation on vigilance behaviour (for example Alberts 1994, Rose & Fedigan 1995, Boinski et al. 2003, Macintosh & Sicotte 2009); however, if they had separated vigilance into categories similar to this study, stronger effects may have been observed.

The foraging/vigilance trade-off suggests that when an animal increases time spent vigilant there should be less time available for foraging (Hill & Cowlishaw 2002). Therefore, if vigilance varies spatially, so should activity budgets. This suggests that the next step in understanding how factors such as spatially varying predation risk affect the foraging/vigilance trade-off is to try to investigate spatial variation in activity budgets.

This chapter represents the culmination of the collection, analysis and interpretation of detailed data concerning a variety of samango monkey anti-predator behaviours. Using these data it was possible to investigate the effects of predation risk on vigilance behaviour at a level of detail not previously attempted on an arboreal monkey species. The approach used is original in its use of GIS techniques to create landscapes of vigilance and spatial regression analyses to investigate the simultaneous effects of various environmental and behavioural factors on vigilance behaviour.

Chapter 8

Discussion

To survive and reproduce animals are forced to balance the time they attribute to biologically important activities which cannot be performed simultaneously (Dunbar 1992). One such trade-off is between foraging and predation risk, where individuals are often forced to balance the often conflicting activities of foraging and minimising risk (Underwood 1982, Lima 1998). The main aim of this study was to investigate how samango monkeys adapt behaviourally to spatially and temporally varying resources and risk. The results showed that factors such as a seasonally variable climate and spatially varying perceived eagle predation risk can have very important influences. The purpose of this chapter is to review and evaluate the main findings of this study, before suggesting some potential avenues of future research.

8.1 Seasonal effects on diet

Samango monkeys are the most southerly ranging, primarily arboreal, African monkey species (Wolfheim 1982). At such latitudes they must survive highly seasonal climates often with periods of cold temperatures and prolonged periods of low rainfall (Willems 2007). Due to varying food availability and other environmental conditions an expectation was that diet should vary with season (Conklin-Brittain et al. 1998, Wrangham et al. 1998), as well as between populations in equatorial locations and those further south (Hill & Dunbar 2002). Using linear correlation analyses data on monthly climatic variation were compared to seasonal changes in

diet composition (Chapter 3). A surprising result of these analyses was that time spent feeding on fruit showed no significant variation seasonally, whereas time spent feeding on leaves increased during winter months. As overall time spent feeding also increased in winter, it appears that the samangos increase their overall food intake during the colder months. There are several possible reasons for the increase in food intake (Iwamoto & Dunbar 1983, Garber 1993, Doran 1997), but the most feasible is the extra energy required to survive colder conditions (Iwamoto & Dunbar 1983). Testing this hypothesis would be difficult, due to the difficulty in calculating energy expenditure. However, one option would be to analyse the nutritional content of the food consumed to test for increased calorific intake during these months.

Leaves contributed 43.9% of the focal group's diet during the study period; and leaves contribute a large amount to samango diets (>25% of total diet) in several different locations, such as Uganda (Fairgrieve & Muhumuza 2003, Twinomugisha et al. 2006), Malawi (Beeson et al. 1996) and elsewhere in South Africa (Lawes 1991). These results show that samangos generally consume a higher proportion of leaf matter in their diet than other arboreal guenons (Chapman et al. 2002). Samangos have longer caecums, larger numbers of cellulases and more cellulose digesting bacteria than other Cercopithecines (Bruorton et al. 1991). This potential diet flexibility may be an important contributor to their large species distribution, as species with large distributions are often diet generalists in order to adapt to varying environmental conditions (Verberk et al. 2010, Verberk 2012).

The large distribution occupied by samangos was examined further in an investigation into the effect of climatic variables on diet composition on a geographical scale (Chapter 4). This was achieved by taking data from 12 long-term study populations of samango monkeys from various locations throughout sub-Saharan Africa and comparing their diet compositions with climatic variables. The results indicated that temperature seasonality had significant effects on the proportion of both fruit (positive relationship) and animal matter (negative relationship) in samango monkey diet. There was no evidence from these analyses

that proportion of leaves in the diet varied spatially. It appears that the samangos increase the proportion of fruit in their diet and decrease their feeding on animal matter further south. There is no reason to think that fruit availability increases further south (Ting et al. 2008), but competition for fruit may decrease, due to decreased primate species richness (Eeley & Foley 1999). With fewer arboreal monkey species competing for fruit, samangos occupying southerly latitudes may be able to increase the proportion of fruit in their diet. Higher seasonality at these locations may mean that variation in fruit availability is higher on a seasonal basis (Ting et al. 2008), and the samangos' ability to supplement their diet with leaves may allow them to survive harsh winters or periods of low rainfall (Hanya et al. 2011). Therefore, samangos' ability to be flexible in their diet may be an important determinant of their ability to survive in more southerly latitudes than other guenon species (Hanya et al. 2011). The findings of this study have highlighted the importance of studying populations at the edge of a species' distribution, in order to investigate the magnitude to which they are forced to adapt behaviourally to often difficult environmental conditions (Sexton et al. 2009).

The biogeographical approach used (Chapter 4) has potential uses in the field of conservation. For example, mapping the distributions of ecological factors and comparing them to climate variables will allow an investigation of how changes to climate variables to levels predicted by climate change theory would affect primate behaviour and distribution (Dunbar 1998, Korstjens et al. 2010, Lehmann et al. 2010). This might be useful in understanding how best to preserve certain habitats. For example, if a species is likely to increase its fruit feeding with increasing temperature, then reintroducing another fruit feeding species to that habitat might not be the best option.

8.2 Spatial utilisation

The landscape at Lajuma provides a mixture of habitat types, with variation in food availability, visibility and canopy height (Chapter 5). The samangos on site form groups, defend territories aggressively and experience predation risk from several species. With resources and risk varying over space it was expected that the samangos would use their habitat strategically. Unlike vervets at the same study site (Willems & Hill 2009b), the samangos showed no evidence of spatially perceived leopard or baboon predation risk, but avoided areas considered high potential eagle risk. These studies show similar species, sharing similar ranges, may experience very different predation pressure, which suggests some interesting implications. Samangos are primarily arboreally adapted, whereas vervets are semi-terrestrial (Anapol et al. 2005). By spending time terrestrially, vervet monkeys increase their predation risk from leopards and baboons, as shown by a high perceived leopard and baboon predation risk at Lajuma (Willems & Hill 2009b). However, due to their ability to move quickly on the ground they may have a higher escape chance from such predators than if they were adapted entirely for arboreal living. In this situation the nearest tree might still be the best escape route and the ability to outmanoeuvre terrestrial predators in the trees would be an advantage, which may explain why arboreal characteristics such as long tails are still present in vervet monkeys (Anapol et al. 2005). With regard to eagle predation, predation risk may be higher further up in the trees, but samango monkeys have a better ability to escape because of their physical adaptations. Therefore, the evidence from this study and Willems & Hill (2009b) suggest that at Lajuma there are two specific niches, one for an arboreal monkey species which can survive a relatively high risk from eagle predation, and another for a semi-terrestrial species which can move quickly on the ground but can still move relatively well higher in the canopy. Without the presence of the different predators the two different niches might not exist. This is an example of how a healthy predator community can help maintain prey diversity, which has further repercussions in fields such as conservation, with regard to keystone species (Chesson 2000).

The landscapes of fear created in Chapter 5 detail horizontal spatial variation in perceived risk. However, Emerson et al. (2011) were able to observe variation in perceived risk along a vertical scale. These factors could be combined to investigate spatial behavioural variation of perceived risk in three dimensions. 3-D landscapes would allow a detailed view of how animal behaviour, particularly of arboreal species, varies over their entire range. With advances in behavioural observation methods resulting in detailed data and the continuing development of GIS software, 3-D landscapes are the next logical step for this powerful ecological tool. A recent study used giving-up density experiments to create a 3-D landscape of fear for vervet monkeys (Makin et al. 2012). The study found that vervets are forced to vary their 3-D space use dependent upon perceived predation risk from both terrestrial and arboreal predators. As used by Emerson et al. (2011), GUDs provide a useful tool for investigating perceived risk on a vertical scale; however, they have their limitations over large areas. Therefore, the methods used in Chapter 5 for calculating perceived horizontal predation risk combined with giving-up density data for vertical risk, would provide an excellent option for creating 3-D landscapes of fear. An additional useful step would be the combination of these landscapes with data on predator utilisation distributions and behavioural spatial variation. By looking at both the predator and prey's landscapes in tandem, it would be possible to interpret and evaluate the variation in behaviours of both species.

The landscape of fear approach also has some interesting possibilities for the investigation of the different anti-predation responses of mixed species assemblages. The comparison of the samango and vervet landscapes of fear provided some very interesting outcomes; however, further comparisons could be made by including landscapes of fear for other species. Using Lajuma as an example, an interesting study would be to include, where possible, the landscapes of fear for bushbuck, red duikers, crested guineafowl and rock hyrax. This would allow the investigation of questions such as, do species which are subject to risk from the same predator species have similar landscapes of fear? The further inclusion of the utilisation distributions of the main predators would then allow for a total, multi-species investigation of space use.

I feel that Lajuma presents an ideal location for such a study, because of the presence of a variety of predators and prey species from a number of different taxa. The understanding of such species interactions and interdependence could have vital implications for the understanding of ecosystems and how best to conserve them (Franklin 1993, Sinclair & Byrom 2006).

8.3 Vigilance behaviour

Several factors can cause an individual to be vigilant, including predation risk or the risk of aggressive encounters with conspecifics (Roberts 1996). The aim of this study was to investigate at what level these factors affect vigilance behaviour within the study group. Variation in behavioural (height of focal individual, activity, number of nearby individuals) and environmental variables (hour of day, mean monthly temperature) were used to investigate variation in vigilance behaviour (Chapter 6). To achieve the thorough and appropriate analysis of these data, a custom-made model was constructed, without the assumption constraints of traditional tests (Pawitan 2001, Richards 2008). The main results were that samangos spend more time vigilant and have lower glance rates when resting than when feeding. Increased glance rates whilst feeding indicate that the monkeys attempt to counteract the effect of spending less time vigilant by increasing glance rate (Gluck 1987, Cowlishaw et al. 2004). As height in trees increased so did time spent vigilant, but glance rate decreased. The number of nearby individuals was also an important factor and as this increased time spent vigilant decreased, with no apparent effect on glance rate. This chapter showed that sometimes the usage of traditional modelling approaches is unfeasible for some types of ecological data. Ecological researchers should be made aware of the options available in terms of these custom-made models which potentially provide more reliable results than their parametric alternatives when model assumptions are being violated (Pawitan 2001, Mason et al. 2011, Richards et al. 2011).

Finally I investigated spatial variation in vigilance behaviour and the factors which influence it (Chapter 7). Landscapes of vigilance were created for each vigilance category to examine spatial variation in looking upwards or downwards. Utilising linear correlation analyses and mixed regressive-spatial regressive models, independent variables such as perceived eagle predation risk, number of nearby individuals and visibility were used to predict spatial variation in these vigilance categories and also glance rate. The results showed that in areas considered high eagle predation risk the focal individuals spent more time looking upwards. Similarly to the results of Chapter 6, time spent vigilant decreased in the presence of more nearby neighbours. The prediction that visibility would affect vigilance behaviour was not supported. No previous study has attempted to investigate spatial variation in primate anti-predator in such detail and the results provide an interesting insight into how a Cercopithecine monkey species confronts the foraging/risk trade-off. The findings of this study indicate that predation risk is vitally important factor determining how samango monkeys approach many aspects of their lives. Therefore, any study investigating variation in samango behavioural ecology, and Cercopithecines in general, must consider the potential effects of perceived predation risk before making any judgements (Hill & Dunbar 1998, Willems & Hill 2009b). This study has added to the understanding of predation as a previously important and continuing contributor to primate evolution (van Schaik 1983, Anderson 1986, Zuberbuhler 2007).

The use of the landscapes of vigilance in Chapter 7 have highlighted an interesting conundrum regarding the term “landscape of fear”. During 96 follow days only 59 eagle specific alarm calls were recorded. This suggests that alarm calls were used by the samangos not to highlight the presence of perceived risk, but as a response to an observed predator. Therefore, the “landscapes of fear” in Chapter 5 may not actually be a representation of perceived fear or risk, but may represent actual risk. This makes me consider that perhaps the term “landscape of fear” is incorrect in this instance. In contrast, the landscapes of vigilance are an indication of how the samangos continuously vary their anti-predator behaviours. In areas of higher risk, it

appears that the samangos increase their vigilance. The landscapes of vigilance are therefore perhaps a more accurate representation of spatially varying fear than the landscapes based on alarm calls. The mapping of alarm calls is a useful tool for understanding how predation risk for a primate group may vary spatially. However, with such methods it is extremely difficult to recognise whether the calls were reactionary, due to the definite presence of a predator, or preventative, due to increased fear. An interesting thought for future studies which intend to use the term "landscape of fear" is for them to try to consider whether their landscapes are actually representing fear, or is what is being observed a landscape of risk and response?

8.4 Methodological limitations

In hindsight there are a range of improvements I would have liked to have made to my data collection and analysis. The fruit availability calculation used throughout the thesis could have been improved in a number of ways. The estimations would have benefitted from extending the data collected in the phenological transects. Firstly the inclusion of more species, including *Mimusops zeyheri*, would have been beneficial; as well as increasing the number of individuals of each species sampled to at least 20. During data collection a measurement of circumference of trunk at a height of one metre was collected. Unfortunately due to an error in applying the phenological methodology by a field assistant there were inaccuracies in the data set that meant it could not be incorporated in to the analysis. This measurement is used in many studies investigating plant development (e.g. Chapman et al. 1992, Felton et al. 2003, Willems 2007), but due to its omission from my data, the comparison of plant data with other studies was made unfeasible.

Throughout this project I have attempted to use the best statistical methods available for the analyses required. However, it was often difficult to use these methods without breaking some of their statistical assumptions. The model constructed in

Chapter 6 for the vigilance analyses was a custom made statistical model, with none of the assumption restrictions of traditional models. These customised models are a potentially powerful tool for ecological studies, because of their ability to accurately and reliably analyse datasets, which often do not meet the statistical assumptions of the non-customised options available. Some of the analyses used in the thesis also used multiple correlation analyses, which many consider problematic (e.g. Holm 1979, Bland & Altman 1995b). However, Nakagawa (2004) argues that multiple testing need not be a problem if the relationships being observed also have high effect sizes. Therefore, the decision was made to only consider relationships significant if they had an effect size higher than 0.5. Although not an ideal solution to the problem of multiple testing, this method allowed for the thorough interpretation of the results with a reduced risk of Type I errors.

Another element of my research I was unable to investigate to the level of detail I would have liked, was the samangos' response to leopards. It would have been useful to attempt some playback experiments to investigate whether the Lajuma samangos use specific alarm calls to potential leopard threats; however, due to time constraints, this was not possible. With the existence of a leopard specific alarm call of a samango population in Uganda (Papworth et al. 2008), the further investigation of the potential of such a call in the Lajuma samangos is something which definitely merits further investigation.

At Lajuma there were two habituated groups of samango monkeys, which shared a territorial boundary. Although time definitely did not allow it, it would have been useful to have spent a few days a month with the second group, which would have allowed some interesting comparative analyses. For example, it would have been interesting to investigate whether the eagle landscape of fear present in my focal group was also present in the second group. Very few study sites have two such habituated groups in close proximity, and a comparative study would be an excellent option for future work.

8.5 Conclusions

The focal group is part of a population near the southern limit of the most southerly ranging African, primarily arboreal, monkey species and therefore often experience difficult environmental conditions. To survive these conditions they are forced to strategically balance the foraging/risk trade-off, on temporal and spatial scales, both in terms of resource acquisition and avoiding predation. Specifically this thesis has highlighted the important role predation risk plays in the lives of a group of arboreal guenons. Great effort is put into avoiding areas of potentially high risk, maintaining group cohesion and maintaining an adequate level of vigilance throughout the day. All of this must be achieved whilst combating rival groups and maintaining a territory, ensuring adequate food can be foraged and ensuring the successful raising of the next generation. This predation pressure is therefore inevitably a strong driver of the evolution of a range of different features, both morphological and behavioural (van Schaik 1983, Anderson 1986, Zuberbuhler 2007).

"Be vigilant, for nothing one achieves lasts forever"
(Tahar Ben Jelloun, Moroccan poet, 1944-)

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